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THE BOTANICAL GAZETTE

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THE

BOTANICAL GAZETTE

EDITOR
JOHN MERLE COULTER

VOLUME LV

JANUARY–JUNE, 1913

WITH TEN PLATES AND ONE HUNDRED AND THIRTY FIGURES

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TABLE OF CONTENTS

		PAGE
The climax forest of Isle Royale, Lake Superior, and its development. I. Contributions from the Hull Botanical Laboratory **165** (with map and fourteen figures) - - - - - -	*William S. Cooper*	1
Progressive and retrogressive changes in the plant associations of the Delaware Coast (with six figures) - - - - - - - - - -	*Laetitia M. Snow*	45
Ray tracheids in the Coniferales (with plates I and II) - - - - - - - - - -	*Ruth Holden*	56
The life history of *Gloeotaenium* (with plate III) -	*Edgar N. Transeau*	66
Hydrodictyon africanum, a new species. Contributions from the Hull Botanical Laboratory **166** (with six figures) - - - - - - - -	*Shigéo Yamanouchi*	74
Revegetation of a denuded area (with two figures)	*H. S. Conard*	80
The morphology of *Araucaria brasiliensis* (with eleven figures and plates IV and V) -	*L. Lancelot Burlingame*	97
The climax forest of Isle Royale, Lake Superior, and its development. II. Contributions from the Hull Botanical Laboratory **165** (with sixteen figures) - - - - - - - -	*William S. Cooper*	115
Macrozamia Moorei, a connecting link between living and fossil cycads. Contributions from the Hull Botanical Laboratory **168** (with twelve figures) - - - - - - -	*Charles J. Chamberlain*	141
A protocorm of *Ophioglossum*. Contributions from the Hull Botanical Laboratory **167** (with thirteen figures) - - - - - - - -	*L. C. Petry*	155
Inheritance of flower size in crosses between species of *Nicotiana* (with plates VI–X) - - -	*E. M. East*	177
The climax forest of Isle Royale, Lake Superior, and its development. III. Contributions from the Hull Botanical Laboratory **165** (with twenty-five figures) - - - - - - - - -	*William S. Cooper*	189
Studies on the phloem of the Dicotyledons. Contributions from the Hull Botanical Laboratory **169** (with plate XI and three figures) - -	*Ansel F. Hemenway*	236

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PAGE

Paraffin blocks for growing seedlings in liquid culture solutions (with three figures) - - *Conrad Hoffman* 244
The effect of certain chlorides singly and combined in pairs on the activity of malt diastase - - *Lon A. Hawkins* 265
A physiological and chemical study of after-ripening. Contributions from the Hull Botanical Laboratory 170 - - - - - - *Sophia Eckerson* 286
The California Paroselas (with five figures) - - *S. B. Parish* 300
The effect of some Puget Sound bog waters on the root hairs of *Tradescantia* - - - - - *George B. Rigg* 314
Toxicity of smoke. Contributions from the Hull Botanical Laboratory 171 (with four figures) *Lee I. Knight* and *Wm. Crocker* 337
Western plant studies. I - - *Aven Nelson* and *J. Francis Macbride* 372
Sir Joseph Dalton Hooker - - - - - - *F. O. Bower* 384
The Lichens of Mt. Rose, Nevada - - -*Albert W. C. T. Herre* 392
Toxic inorganic salts and acids as affecting plant growth - - - - *Chas. B. Lipman* and *Frank H. Wilson* 409
The transpiration of apple leaves infected with *Gymnosporangium* (with one figure) *Howard S. Reed* and *J. S. Cooley* 421
Undescribed plants from Guatemala and other Central American Republics. XXXVI - - *John Donnell Smith* 431
Vegetative reproduction in an *Ephedra*. Contributions from the Hull Botanical Laboratory 172 (with five figures) - - - - - - *W. J. G. Land* 439
Protoplasmic contractions resembling plasmolysis which are caused by pure distilled water (with six figures) - - - - - - - - - *W. J. V. Osterhout* 446
Reproduction by layering in the black spruce. Contributions from the Hull Botanical Laboratory 173 (with six figures) - - - - - *George D. Fuller* 452

BRIEFER ARTICLES—

A simple revolving table for standardizing porous cup atmometers (with one figure) - - - *G. E. Nichols* 249
Poisoning by *Ginkgo* - - - - - - - *Anna M. Starr* 251
A new wood-destroying fungus (with six figures) - *Adeline Ames* 397
A safety razor modified for cutting hand sections (with one figure) - - - - - - - *J. P. Givler* 399
On *Stemonitis nigrescens* and related forms - - *W. C. Sturgis* 400
Thomas Howell (with portrait) - - - - - *Huron H. Smith* 458
The Seeding of *Phyllocarpus* (with one figure) - *T. D. A. Cockerell* 460

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PAGE

CURRENT LITERATURE - - - - - - - 85, 167, 252, 327, 402, 461

For titles of book reviews see index under author's name and reviews

Papers noticed in "Notes for Student" are indexed under author's name and subjects

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ERRATA

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P. 330, line 9 from bottom, for (fig. 5) read (fig. 3).

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P. 79, line 7 from bottom, for Yamonouchi read Yamanouchi.
P. 186, table V, column 5, for 264.4 read 226.4.
P. 225, legend of fig. 54, for burned read burn.
P. 331, line 9 from top, for C. T. ORTON read C. R. ORTON.
P. 395, line 15 from top, for *Leconora* read *Lecanora*.
P. 402, footnotes [3] and [4] should be interchanged.

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THE

BOTANICAL GAZETTE

JANUARY 1913

THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. I

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH MAP AND FOURTEEN FIGURES)

Introduction

Eastern North America north of Florida and Mexico is divided into two great phytogeographic regions, the eastern deciduous forest and the northeastern conifer forest. In each of these a number of lines of succession may be traced, all those of a region leading to a certain forest type as the final or climax stage. This final type in its large features is determined by climate, and is much the same throughout the region which it dominates. In the eastern deciduous forest the climax type is made up of *Acer saccharum* Marsh (sugar maple) and *Fagus grandifolia* Ehrh. (beech), with the addition of various other species in some portions of the country. The nature of the climax forest of the northeastern conifer region has not hitherto been determined.

Isle Royale lies just within the limits of the northeastern conifer region, barely within, for one of the farthest outposts of the deciduous forest is located on its southwestern end, where there is a considerable area dominated by the sugar maple, in mixture with more northern trees. Except for the maple and a few of its companion species, the flora of Isle Royale belongs strictly to the northeastern conifer region.

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The purpose of the present work was to determine the climax forest of Isle Royale, its composition and character, and to trace the various lines of succession leading to it. It is thus a successional study of a small component portion of the northeastern conifer forest.

At the beginning of the investigation Isle Royale was selected as a field of study because it shows transitional features between the two great forest regions, my original purpose being to devote particular attention to the relations between the conifers and the maple. Circumstances made it impossible to give adequate study to the region dominated by the latter, therefore the work developed into an investigation of the balsam-birch-spruce forest (the northeastern climax) and its attendant successions. For a study of the northeastern conifer forest a more centrally located area might have been preferable; for instance, at some point midway between Lake Superior and James Bay. It will be shown, however, that Isle Royale affords a very fair sample of the forest growth of the northeastern region. It also possesses certain very important advantages which would be lacking in a more centrally located area. Because of its insular position the forest has been less liable to destruction by fire, and the many bays and channels separating various portions of the main island and the outlying islets have served as effective barriers against its spread. Though they have occurred many times during the island's history, it is certain that fires have been far less frequent and destructive here than upon the mainland. The forest may thus be studied in a condition that is as near to being undisturbed as will be found anywhere. Comparative freedom from the destructive agency of man is a second advantage. Again, the island has had a simple physiographic history during the present vegetative cycle, and thus the relation of vegetation to physiography may be the more readily made out. Further, the proximity of the lake shores permits the observation of the earliest stages in the establishment of vegetation upon the rock surfaces, these stages being frequently absent or poorly developed in an inland locality. Finally, the fact that the field of study is an island gives definiteness to the area covered by the investigation.

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Headquarters were established at the Park Place Hotel on Rock Harbor (sec. 4, T. 66 N., R. 33 W.), and field investigations were carried on upon the island during the summers of 1909 and 1910. Most of the detailed work was done in the vicinity of Park Place, but the coast was visited from Hawk Island to Blake Point on the northwest, and from Blake Point to the head of Siskowit Bay on the southeast. Excursions into the interior were made from various points along this stretch of shore.

The study was undertaken at the suggestion of Dr. HENRY C. COWLES of the University of Chicago. I wish to express my appreciation of his invaluable assistance and co-operation, freely given at all times during the progress of the investigation. I desire also to extend my thanks to Dr. M. L. FERNALD of the Gray Herbarium of Harvard University, who determined all doubtful spermatophytes and pteridophytes, and to Miss EDITH A. WARNER of Brooklyn, N.Y., who determined the mosses collected upon the island, about 80 in number. The nomenclature of the pteridophytes and spermatophytes is that of the seventh edition of GRAY'S *Manual*.

PREVIOUS BOTANICAL WORK UPON ISLE ROYALE

A limited amount of botanical work of taxonomic and ecological nature has been done upon Isle Royale. In 1848 W. D. WHITNEY, acting as naturalist for a government exploring party, made a brief list of plants found upon the island, which was published in the report of the expedition (**24**) in 1851. In 1890, according to ADAMS (**4**), F. E. WOOD made a collection of plants in the vicinity of Rock Harbor and presented them to the University of Michigan. In 1901 W. A. WHEELER (**58**) published a list of noteworthy species, reporting for the first time the strange occurrence of *Fatsia horrida* (devil's club) upon the island.

In 1904 and 1905 Isle Royale was visited by parties from the Museum of the University of Michigan, both equipped for ecological work among plants and animals. The first, under the leadership of Dr. A. G. RUTHVEN (**3**), spent three weeks upon the island, after a month's work in the Porcupine Mountains of the northern peninsula of Michigan. Their explorations were confined to the

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southwestern end of the island. In respect to the vegetation the results of this expedition consist in scattered ecological notes and a list of plants including only 91 species (**49**).

The second party, headed by Dr. C. C. ADAMS, devoted all its time (about six weeks) to Isle Royale, and the resulting report is incorporated in a volume of more than 400 pages (**4**). The botanical work was done by HOLT (**33**), whose report comprises a ten-page account of the plant societies, and an annotated list of lichens, mosses, ferns, and seed plants, including 364 species. There is also much of ecological value to be found in the sections by ADAMS, and the report by GLEASON upon the ecology of the invertebrates (**29**).

Two papers by the present writer (**12, 12*a***) should also be mentioned, as they were suggested by observations upon Isle Royale.

TOPOGRAPHY AND PHYSIOGRAPHIC HISTORY

Isle Royale is situated in the northwestern part of Lake Superior in lat. 48° N., long. 89° W., about 25 km. distant from Thunder Cape, which is the nearest point of the Canadian mainland. The island is elongated, extending northeast and southwest, and its dimensions are 72 km. by 14 km. at the widest part. It is formed of several parallel ridges which are made by the resistant centers of successive outcrops of a series of Keweenawan lava flows. These dip southeastward at angles varying from 5° to 40°. The southeast slopes of the ridges are gentle, corresponding with the dip of the beds, while the northwest faces are steep and broken, often precipitous. Several of them extend into the lake at either end of the island as promontories or rows of small islands (fig. 1). The largest, the Greenstone Range, stretches the whole length of the island, and is continued northeastward in Passage Island and Gull Rocks. At several points it reaches an altitude of more than 150 m. above the lake level. Between the ridges are narrow valleys, corresponding with the less resistant peripheral portions of the flows and the sedimentary layers that are interbedded with them. These contain many lakes, and where submerged at the ends of the island form narrow fiord-like harbors and channels. The drainage is well adjusted to structure, the streams flowing along the strike

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of the less resistant beds, entering the lake at the ends of the valleys, or occasionally through narrow cross valleys, most of which are due to faults.

The quaternary history of Isle Royale is briefly as follows: At the beginning of the glacial period the topography, produced during a long period of subaerial erosion, was essentially as now. The ice completely covered the island, moving southwestward nearly with the strike of the beds, but wrought only slight modifications in the topography. Rock basins were excavated in the

FIG. 1.—Southeast across Scovill Point and the outer islands from the slope of the Greenstone Range: Tobin's Harbor in the foreground; Rock Harbor beyond; Lake Superior in the distance.

valleys and many surfaces were smoothed and striated. *Roches moutonnées* are common. Of the little drift that was left behind most was dropped upon the southwest end, and practically all has been rehandled by the waters of the successive postglacial lakes.

Upon the retreat of the ice, Isle Royale was left entirely submerged beneath the waters of Lake Duluth. The remaining history records a gradual emergence corresponding with the repeated changes of the water level as the lake found successively lower outlets. That this emergence was frequently interrupted is shown by the beaches, sea cliffs, and wave-cut terraces that occur at various altitudes, corresponding with similar ones along the

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mainland coast. These indicate periods when the water level was stationary for a considerable time. According to LANE (36) the present shore line is more strongly marked than any at higher levels. "Nor is it surprising," LANE remarks, "that the lake level should now be tolerably constant, for Lake Superior now drains over a rock threshold." In comparatively recent post-glacial time (since the formation of the very recent Nipissing beach) tilting occurred in the Lake Superior region, with uplift northward. This must have modified more or less the drainage conditions upon Isle Royale. It is important to bear in mind the self-evident fact that never since its first emergence from the waters of Lake Duluth has Isle Royale been connected with the mainland.

For further geologic and physiographic details the reader is referred to LANE's report (36), to which I am indebted for the material for this brief sketch; and also to ADAMS (4), who discusses the physiographic history of the island with considerable fulness. ADAMS also gives much valuable data concerning the influence of the lake storms and surface currents upon the biota of the island.

PHYSIOGRAPHIC AGENCIES NOW AT WORK

The agencies that are now modifying the surface of the island, which are of course the same that have been active throughout its history, may be considered under two heads.

Among the DESTRUCTIVE agencies, *weathering* is of the greatest importance in its influence upon vegetation. It is most evident upon the steep northwest slopes of the higher ridges. Here there are somewhat extensive talus piles lying at the bases of cliffs, or in some cases occupying the whole slope, the cliff having been buried by the accumulation of fragments. In many places the talus is fully clothed with climax forest, in others the fragments are bare or merely lichen covered. The results of weathering are evident also upon the bare rock shores, where scales and plates are seen to have been split from the rock surfaces through the agency of temperature changes. Very important, though effectually concealed, is the chemical action which is going on beneath the humus carpet that covers most of the island's surface. Between the humus and the bed rock there is nearly everywhere a layer of

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small rock fragments mixed with organic matter. Most of these fragments are so decomposed that they can be cut easily with a knife. The bed rock itself frequently shows the effect of chemical action. Vegetation is here seen as an important physiographic agent.

Stream erosion is of trifling importance upon Isle Royale because of the small size and low gradient of most of the streams and their freedom from transported materials, necessary as agents of abrasion.

Wave erosion is the most conspicuous of destructive agencies. The surf is actively cutting into the land, and the shore features at the present lake level are very pronounced. At many points along the southeast coast the normally gentle slope of the shore has been transformed into terrace and cliff. In some parts of the abrupt northwest shore the waves are undermining the climax forest itself. In connection with erosion by waves should be mentioned the work of ice, the precise effects of which could not be determined in summer study.

Under the head of CONSTRUCTIVE agencies come deposition by streams, waves, currents, and vegetation. The only notable instances of stream deposition are the few deltas, the materials for which were derived largely from the glacial drift and the products of wave erosion at former levels. The subject is treated further under the head of "Delta swamp succession." The fragments eroded by waves are deposited in the form of beaches and bars, in coves and harbors. Shore currents are effective in transporting the material, and in sweeping the finest into sheltered bays, where it is dropped in the quiet waters. The work of vegetation consists in the formation of peat and humus. Plant life here again appears as a physiographic agent of great importance.

CLIMATE

ADAMS (4, pp. 41–44) has described in some detail the climate of the general region, his data being obtained from the records of the Weather Bureau at Port Arthur. The following summary (table I) is derived partly from ADAMS' account and partly from more recent data from Port Arthur obtained through the courtesy of the Canadian Weather Service.

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TABLE I

NORMAL TEMPERATURE AT PORT ARTHUR FOR THE 20 YEARS 1888–1907

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
° C.....	−13.9	−13.7	−7.2	1.7	7.7	13.6	16.8	15.6	11.6	5.3	−2.8	−9.8	2.1

The average maximum temperature for the ten years 1896–1905 was 30.1° C.; the average minimum for the same period was −34.9° C. The mean monthly temperature was below 0° C. for five months, and the mean monthly minimum below 0° C. every month except June, July, and August. The growing season is thus short, including about four months, or even less, between the middle of May and the middle of September. The long northern period of daylight compensates somewhat for the short season.

TABLE II

NORMAL PRECIPITATION AT PORT ARTHUR FOR THE 20 YEARS 1888–1907

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
cm.....	1.77	1.31	2.44	4.18	5.56	7.67	9.82	7.77	8.23	6.49	3.15	1.77	60.16

It is here seen that the greater part of the precipitation takes place during the growing season; 39.05 cm., or more than three-fifths of the total, occurs during the months May–September. The snowfall is rather light; during the six years 1900–1905 the average was 61.03 cm. Reduced to water this amounts to a precipitation of 6.1 cm., which is about one-tenth of the average total for that period.

The evaporation rate is doubtless low because of the low temperature, but there are no data available. This and the relatively abundant precipitation during the growing season seem adequate to account for the extreme mesophytism of the forests of the region.

Since 1906 temperature and precipitation records have been kept during the season of navigation by Captain MALONE at the lighthouse on Menagerie Island. This is one of the Isle Royale archipelago situated 4 km. distant from the nearest point of the main island. During the summer of 1910 I kept thermograph and rain gauge records at Park Place. There is therefore opportunity

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for a partial comparison of the insular climate with that of the mainland. Summarization of the records for Port Arthur, Park Place, and Menagerie Island gives the following results:

TABLE III

TEMPERATURES ° C.

		June	July	August
Port Arthur	Mean maximum	23.4	23.9	21.3
	Mean minimum	10.4	11.7	10.0
	Mean daily range	13.0	12.2	11.3
Park Place	Mean maximum	....	21.4	21.4
	Mean minimum	....	12.4	12.9
	Mean daily range	....	9.0	8.5
Menagerie Island	Mean maximum	17.0	18.8	19.4
	Mean minimum	7.1	10.5	13.1
	Mean daily range	9.9	8.3	6.3

From this table we see that the maxima upon Isle Royale are lower than upon the mainland, during the summer at least. Menagerie Island, most under the lake's influence, is the lowest, and Park Place, upon the main island, is intermediate. We may infer that as a result of lower temperatures the evaporation is less upon Isle Royale. ADAMS (4, p. 44) suggests that insular location and imperfect drainage probably operate to reduce evaporation. The table also shows that the Isle Royale climate is characterized by less pronounced daily temperature changes than is that of the mainland. The daily range is shown to be uniformly greatest at Port Arthur, intermediate at Park Place, and least at Menagerie Island.

A further comparison (table IV) brings out the fact that the proximity of the lake retards the opening of the growing season, but also that the same factor prolongs it into the fall.

TABLE IV

MEAN MONTHLY TEMPERATURES (° C.) MAY–NOV.; AVERAGE 1906–1909

	May	June	July	August	Sept.	Oct.	Nov.
Port Arthur	7.9	13.6	16.9	15.9	11.6	5.7	−1.7
Menagerie Island	4.3	8.9	11.6	14.4	12.6	6.8	1.9

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Evidencing the retardation of the season is the fact that ice frequently remains in sheltered places on the northwest coast of the island into July. I have seen a deserted mine shaft filled solid with ice on July 4. FOSTER and WHITNEY report ice "under the shade of crags, and among the thick evergreen swamps of white cedar."

In precipitation there is apparently not much difference between Port Arthur and Isle Royale, at least during the growing season. As far as the records go the mainland has a slight advantage.

TABLE V

AVERAGE PRECIPITATION MAY–NOV., 1906–1909

Port Arthur	48.00 cm.
Menagerie Island	43.74 cm.

From the foregoing data, which unfortunately are rather fragmentary, it appears that there is at present no ground for concluding that the island climate is effective in producing a more mesophytic type of vegetation than that of the mainland, or vice versa. The lower evaporation rate upon the island, due to lower temperature, is balanced by a less precipitation during the growing season; and the growing season, although retarded in its commencement upon the island, is apparently as long as upon the mainland. The question cannot fully be settled without fuller precipitation records from Isle Royale and a determination of the actual evaporation rates in the two localities. The data presented, however, indicate, so far as they go, that the insular position of the field of study does not seriously affect its value as a fair sample of the region dominated by the northeastern conifer forest.

Part I.—The climax forest

The forest that completely clothes the surface of Isle Royale, with the exception of a part of the bog areas, some limited stretches of xerophytic character, and the small portion dominated by the maple, is made up largely of three trees: *Abies balsamea* (L.) Mill (balsam fir), *Betula alba* L. var. *papyrifera* (Marsh) Spach (paper birch), and *Picea canadensis* (Mill) BSP (white spruce). The studies embodied in the present paper show that this type is the

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climax forest of that portion of the northeastern conifer region under consideration; in other words, that upon Isle Royale it is the final and permanent vegetational stage, toward the establishment of which all the other plant societies are successive steps. It is the "climatic" forest of the region, permanent while the climate remains essentially as now.

The evidence in support of this conclusion lies along four lines: (1) extreme mesophytism of the forest; (2) its uniformity of development; (3) all successions lead to it; (4) maintenance of equilibrium. These lines of evidence will now be considered in order.

1. MESOPHYTISM.—The balsam-birch-white spruce forest is the most mesophytic of all the plant societies of the island. The truth of this statement will appear during the discussion of other points and so no further treatment is necessary here.

2. UNIFORMITY OF DEVELOPMENT.—In all places where it occurs, whether upon rock surfaces or reclaimed bogs, upon the part most recently emerged from the lake or upon the highest ridge, the dominant forest is essentially uniform in character. The tree species are the same, and they bear everywhere the same relations to each other.

3. ALL SUCCESSIONS LEAD TO THE BALSAM-BIRCH-WHITE SPRUCE FOREST.—In a later portion of this paper the various successions are treated in detail, and it is shown that all end with the establishment of the balsam-birch-white spruce forest. In other words, those phases of the vegetation that are not uniform in character with the main forest mass are plainly tending toward uniformity. The successions upon Isle Royale may be classified as follows:

A. Primary successions
  I. Xerarch[1] successions
    1. The rock shore succession
    2. The beach succession

[1] The terms *xerarch* and *hydrarch* are here used for the first time, for the purpose of indicating a natural and important classification of plant successions. The former is applied to those successions which, having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic in their successive stages; the latter to those which, originating in hydrophytic habitats such as lakes and ponds, also progress toward mesophytism.

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II. Hydrarch successions
  1. The bog succession
  2. The delta swamp succession
B. Secondary succession
  The burn succession

4. MAINTENANCE OF EQUILIBRIUM.—It has been possible to state with brevity the three points that have so far been presented; indeed, to one visiting the island they are almost self-evident. The validity of the fourth is not so plainly to be seen.

Both observational and experimental studies have shown that the balsam-birch-white spruce forest, in spite of appearances to the contrary, is, taken as a whole, in equilibrium; that no changes of a successional nature are taking place within it. Superficial observation would be likely to lead to exactly the opposite conclusion. In the presence of the other good evidences of permanence outlined in the preceding paragraphs, it became necessary to seek for an explanation of the seeming condition of rapid change that was apparently so plain in the forest. The solution was found in the course of a detailed study which included (1) the characteristics and life history of each tree species and of certain of the lower forms which were of importance, and (2) all the processes and changes brought about through the interrelations of the forest species, discovered by intensive study of a number of limited areas of definite size (quadrats), with every available source of evidence laid under contribution; in other words, an attempt at a thorough investigation of the dynamics of the forest. In the following discussion the results will be given under three heads: I. Description of the forest; II. Studies of individual species; III. Quadrat studies.

I. DESCRIPTION OF THE FOREST

For the sake of concreteness I have selected a definite locality for description, bearing in mind, however, that such a thing as a piece of forest of limited extent which is "typical" of the growth of a region hardly exists.

Smithwick Island (sec. 4, T. 66 N., R. 33 W.) was the selection for this description and for particular study, because the outer row of small islands inclosing Rock Harbor had the appearance of

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having been least disturbed by accidental conditions such as fires; and of these islands Smithwick was the most conveniently situated. So primeval and luxuriant is the aspect of the forest here that at first it seemed almost safe to assume that the island had never been burned over since its emergence from the lake. I found, however, in one place, at a depth of one-third of a meter, a layer of carbonaceous material with fragments of charcoal. It is certain then that fire, to an unknown extent, has entered into the history of the island, notwithstanding the many indications to the contrary. Nevertheless, granting that the island may have been burned over at some time, it is plain that the forest has long since returned to its natural condition and may fairly be taken as a suitable area for the study of the climax state. We may be sure that the forest on Smithwick Island has not been disturbed for many hundreds of years at least, and this is not often the case on the main Isle Royale.

There is one somewhat abnormal feature of the conditions surrounding these outer islands that should be mentioned, namely, that the exposure to the strong lake winds is greater than on the main island, and that the death-rate among the trees is thereby increased, and not always proportionally among the different species. On the whole, though, this added exposure merely intensifies certain processes that are in operation everywhere, and thus renders them easier of observation.

The average elevation of Smithwick Island is about 7 m. The southwest one-third was thoroughly burned over about 15 years ago. The forest covers the unburned portion almost completely, being bordered along most of the Rock Harbor side by a narrow shingle beach, and on the lakeward edge by a belt of bare sloping rocks, frequently interrupted by broken or precipitous sea cliffs.

Seen from Rock Harbor the forest has the following appearance, and this description will apply fairly well to the climax forest of Isle Royale in general (fig. 2). The first impression is of great density, the thick foliage extending to the ground at the edge of the forest, allowing no view into the interior. The sky line is ragged, made up of an irregular combination of sharp points and rounded curves, due to the mixture of broad-leaved trees and conifers.

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Above the general level of the treetops tower occasional very old white spruces, conspicuous features in spite of or rather on account of their fewness. The paper birches make considerable show by reason of their thick tops, often appearing to compose at least half of the forest, but in reality not much more abundant than the spruces. The balsams are plainly very abundant, and are actually even more so than they seem, since many small ones are hidden by other trees. There are a few large specimens approaching the spruces in size, and thick groves of medium-sized trees are just

FIG. 2.—Exterior view of the climax forest upon one of the row of islands bounding Rock Harbor on the southeast: two tall white spruces at the right; a group of balsams at the left; several large birches.

visible, their spirelike tips appearing in dense clusters among the birch tops. The forest toward the harbor is bordered by a belt where *Alnus crispa* (Ait.) Pursh (green alder) is common, filling in the gaps between the trees. In this region *Pyrus americana* (Marsh) DC (mountain ash) is also frequent, and *Thuja occidentalis* L. (arbor vitae) is occasional.

Upon entering the forest we seem in many places to be in the midst of a dense growth of nearly pure balsam. The individuals of this species are of all sizes, and there is a pronounced tendency among them to grow in close groups. The small trees (roughly

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those 7 m. high and under) are greatly in excess of the larger ones. There are also numerous dead and dying specimens, almost always small ones, some of the dead trees showing evidence of having succumbed very recently, the needles not yet having dropped off. The occasional large trunks of the birches are conspicuous objects, but young ones are not numerous. It is often difficult to find a single spruce, unless one has carefully estimated from the exterior the position of one of the conspicuous old specimens. Young spruces are exceedingly rare, so that a long search will be necessary to discover one. The shade in most parts, especially under the closely placed balsams, is dense, though there are frequent partial openings, caused principally by windfalls (fig. 3). Standing dead trees of large size are very rare, but fallen trunks in all stages of decomposition are numerous, the greater number being balsams, though the dead birches are more conspicuous on account of their greater size.

FIG. 3.—Illustrates conditions resulting from a windfall in the climax forest: fallen trunks and young balsams; Smithwick Island.

Shrubby growth is not abundant. The areas of not too dense shade are often thickly populated with *Taxus canadensis* Marsh (ground hemlock). Other large shrubs that are more or less frequent are *Alnus crispa* (Ait.) Pursh (green alder), *Viburnum pauciflorum* Raf. (high bush cranberry), *Sambucus racemosa* L. (red-berried elder), *Lonicera canadensis* Marsh (bush honeysuckle), *Fatsia horrida* (Sm.) B. & H. (devil's club), the last abundant in one restricted area.

The herbaceous growth is sparse except in partial openings.

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Most prominent is the association of about eight herbs which is so characteristic of the northeastern conifer forest, and in part of similar forests over a much wider range. The group includes the following: *Cornus canadensis* L. (bunch-berry), *Trientalis americana* (Pers.) Pursh (star-flower), *Linnaea borealis* L. var. *americana* (Forbes) Rehder (twin-flower), *Maianthemum canadense* Desf. (two-leaved Solomon's seal), *Clintonia borealis* (Ait.) Raf., *Mitella nuda* L. (mitrewort), *Aralia nudicaulis* L. (wild sarsaparilla), *Coptis trifolia* (L.) Salisb. (goldthread). These species are found in every part of the Isle Royale climax forest, and many of them in the bog forest, bogs, and along the rock shores as well. Others, less characteristic and abundant, still occur commonly: *Lycopodium annotinum* L. (stiff club moss), *L. obscurum* L. (ground pine), *Phegopteris Dryopteris* (L.) Fée (oak fern), *Aspidium spinulosum* (O. F. Müller) Sw. (shield fern), *Polypodium vulgare* L. (polypod), *Cystopteris fragilis* (L.) Bernh. (fragile fern), *Moneses uniflora* (L.) Gray (one-flowered Pyrola), *Ribes prostratum* L'Her (fetid currant), *Epipactis repens* (L.) Crantz var. *ophioides* (Fernald) A. A. Eaton (rattlesnake plantain), *Oxalis Acetosella* L. (wood sorrel), *Habenaria obtusata* (Pursh) Richards, *Comandra livida* Richards.

By far the most important part of the herbaceous vegetation, both quantitatively and ecologically, is the moss contingent. This forms a nearly continuous carpet, being absent only where the shade is very dense. Three species are chiefly concerned, and these are quite equally distributed, one usually being dominant in a given spot. *Calliergon Schreberi* (Willd.) Grout (*Hypnum Schreberi* Willd.) is perhaps the most abundant, and grows in the drier places alone, as well as mixed with the other two in general. *Hylocomium proliferum* (L.) Lindb. usually covers the areas of well decomposed humus; while *Hypnum crista-castrensis* L. seems to prefer rotten wood. Next to these in abundance is *Hylocomium triquetrum* (L.) Lindb.

The humus soil, which is composed largely of moss remains, tree waste, and rotten wood, varies in depth from 0.25 to 6 dm., the average being perhaps about 3 dm. It rests directly upon the smooth rock surface or is separated from it by a loose layer of decomposed fragments.

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Returning to the trees, the first conclusion would naturally be that we have here a stage in the succession approaching but not having reached the final or climax condition. The spruces and birches appear like relicts, and the balsams, which seem to be of all ages, but mostly younger than the trees of other species, are apparently succeeding them. The seeming probability is that before long the birches and spruces will have died out, leaving a pure growth of balsam which in the future will succeed itself. Appearances of this kind have sometimes been considered sufficient to prove that succession is in active progress, and there are undoubtedly many cases where the phenomena are not deceptive. In no case, however, should the mere appearance of rapid succession be admitted as valid evidence until verified by surer methods of study. The results of an attempt to use such methods are detailed in the two following sections.

II. STUDIES OF INDIVIDUAL SPECIES

ABIES BALSAMEA (balsam fir).—If it be objected that the forest is after all a practically pure stand of balsam, with a mere scattering of other species, the following facts will be sufficient answer. It is true that in number of individuals, all sizes considered, the balsam is greatly preponderant. Of the 254 trees included in the six quadrats soon to be described, 78.7 per cent are balsam. But if we take account only of those trees which may be considered as forming the mature stand, the percentage of balsam becomes much smaller. Size, not age, is here the proper criterion. Considering those trees which are 1.25 dm. and more in diameter, which is a rather low limit to set, the proportion is only 56.7 per cent. Among the larger trees the balsams are still less numerous, making only 33.3 per cent of those 2.5 dm. and more in diameter (fig. 4). The same facts are shown when age is considered instead of size, though in a somewhat less striking manner (fig. 5).

Two causes are responsible for the preponderance of balsam in the young growth. First, the seedlings make a successful start in almost any sort of situation, provided sufficient light be available. Very young seedlings were seen commonly in such diverse situations as the following: natural openings in the forest caused by

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windfall, in moss and humus (by far the commonest situation); windfall opening in cedar swamp, in moss; rotten logs in forest

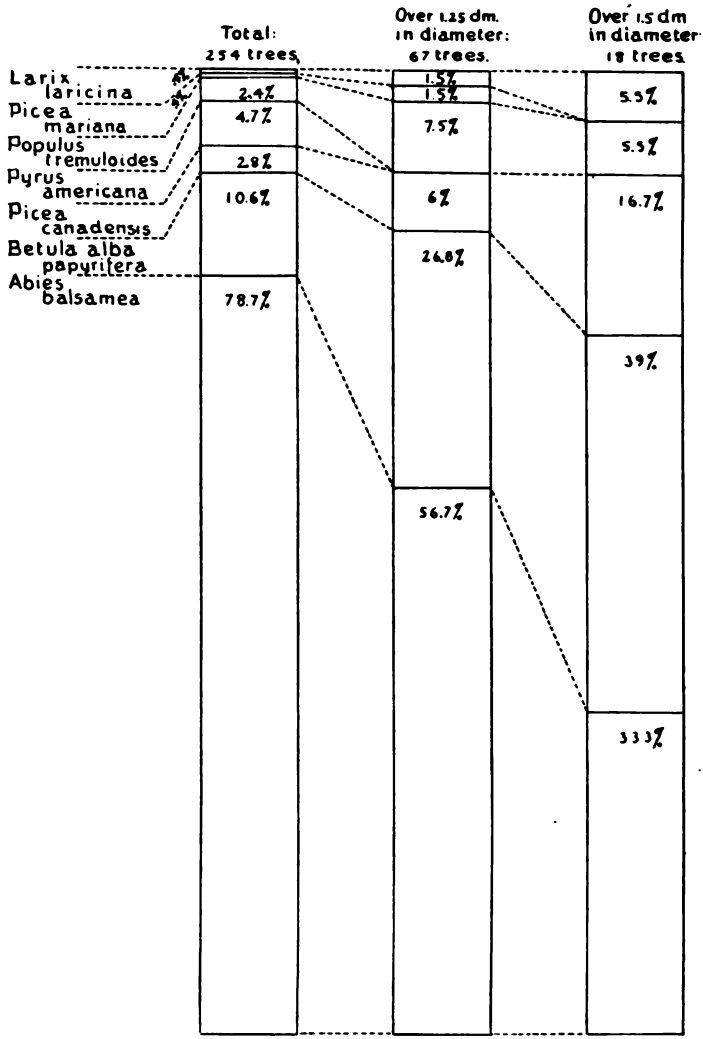

FIG. 4.—Composition of the climax forest; according to size of trees

(infrequent in this region); open bogs in sphagnum; crevices and humus-filled depressions on rock shores; burned areas, both forested and bare, not abundant; upper beach among large shingle,

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in partial shade and entirely open, abundant in one locality; sand bar across mouth of small stream, abundant. The entire absence

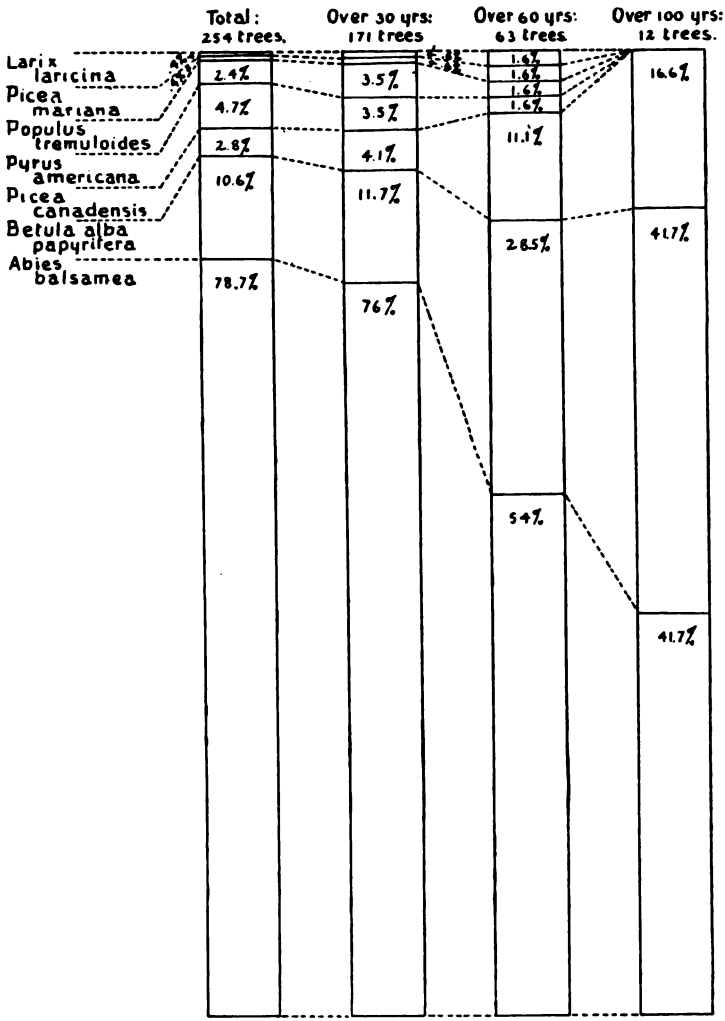

FIG. 5.—Composition of the climax forest; according to age of trees

of very young seedlings wherever the shade is even moderately dense is noteworthy. Later in life the young trees can endure severe shading, but for a successful start abundant light seems to

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be a necessity. The possibility must be admitted that light (or rather radiant energy) is only indirectly the important factor, its influence lying in its effect upon the seed bed. Densely shaded soils upon Isle Royale are nearly everywhere more or less of the nature of peat, low in temperature, soggy with unavailable water, and probably like peat deficient in certain types of bacterial and fungal life. The obvious effects of abundant access of radiant energy would be to partially cure the sogginess of the soil and thus increase its oxygen content, and to bring about a high soil temperature; both of which changes would result in greatly increased activity among the various types of soil organisms. Plans to carry out some experiments with a view toward determining the germination conditions of the balsam and other trees were frustrated by the total failure of the seed crop in 1910.

A second cause, which easily accounts for a considerable part of the young growth of balsam, is found in the habit of layering, by which that species reproduces abundantly. All the other conifers of Isle Royale except the pines possess the habit too, but to a much less degree. In a previous paper (12) I have described in detail the layering habit of the balsam and other conifers, and therefore a few words here will be sufficient. In the forest one frequently comes upon small groups of young balsams, composed often of about half a dozen individuals of various sizes. Upon superficial inspection these would easily pass for a cluster of seedlings, but if the group be carefully dug up it will be found that the young trees are all connected with each other just below the surface of the ground. The group comes into existence in the following manner. One or more of the earliest branches of a young tree (which is sometimes hardly beyond the seedling stage) comes to be slightly covered with humus and litter, and produces roots. The tips then become erect, and taking on radial symmetry are transformed into miniature trees. By successive layering of branches as many as five generations produced in this manner may be included in a single group. Large drooping branches of mature individuals may layer in the same way, and it is not uncommon to find an old trunk surrounded by a circle of daughter trees developed from layered branches. The young shoots soon come to depend entirely

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upon their own root systems for sustenance, and there is evidence that a considerable number of them become independent through the decay of the connecting branch. The habit is so common in the Isle Royale forests that a large proportion of the apparent balsam seedlings may be accounted for in this way.

The preponderance of balsam in the young tree growth being accounted for, it is now necessary to explain its rapid decrease when greater size and age are considered. Several causes combine to bring this about. Abundant germination is itself a disadvantage, since it results in severe competition, much of the stand undergoing suppression and finally death. The species is very susceptible to fungus attacks and to diseases of many kinds. Rotten-hearted trees are very common. Witches' brooms caused by a rust (*Peridermium*) are familiar objects. According to MOORE and ROGERS (41), the liability to fungus attack is greater in pure stands than where trees are scattered. The common group habit of the species is therefore a disadvantage in this respect. The prevalence of heart rot, together with the natural brittleness of the wood, cause extreme liability to windfall, and broken trunks are a common sight, while uprooted balsams are rare. It is not surprising, in view of these facts, that in spite of its prolific power of germination the balsam never reaches the position of dominance in the mature stand. In a word, its high birth-rate is balanced by a high rate of mortality.

BETULA ALBA var. PAPYRIFERA (paper birch).—The prominence of this species in the mature stand and in the general aspect of the forest has been noted, and also its comparative scarcity in the young growth. It is certain that the germination of the birch in this region is far from prolific. Very young seedlings were frequently seen, and in situations almost as varied as those inhabited by the balsam, but never in abundance as in the case of that tree. I quite frequently found very small seedlings in dense shade, but they were never more than five or six years old, indicating that conditions (probably light supply for photosynthesis) were not favorable for continued growth. Opportunity for successful reproduction comes usually, as in the case of the balsam, after windfalls (fig. 8). On account of its much less prolific germination the birch is far less

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abundant in such situations than the balsam. Its growth under the same conditions seems to be somewhat faster, however, and so the few birches of the windfall area, or some of them, soon overtop the balsams and cause the suppression of many of the latter, at the same time, with the aid of the balsams, temporarily preventing further reproduction of either species. Paper birch has comparatively few and ineffective fungus enemies (DANA **18**) and is not particularly susceptible to damage by wind, on account of its elastic branches and extensive though shallow root system. Even when it is broken off in severe storms, as occasionally happens, it has a means of recovery in its ability to send up vigorous sprouts from the stump. Occasional clumps of immense birch sprouts scattered through the forest are evidence of this power. The most effective obstacle to its increase is competition with the balsam in its early stages, and here its greater rate of growth gives it a slight but important advantage. On the whole it may be said with certainty that its low birth-rate is compensated by a very low mortality, and it is thus able to maintain itself in making a good proportion of the mature stand (figs. 4, 5).

PICEA CANADENSIS (white spruce).—This species is ecologically much less important than the first two, occurring only sparingly in most places; but it attains a greater size than the other trees, and is one of the most conspicuous features of the forest. On account of its scarcity little could be discovered concerning its life-history upon Isle Royale. From the few seedlings that were observed it seems probable that abundant light is necessary for its successful reproduction. According to the United States Forest Service (**22**) it is not a prolific seed bearer, and has definite seed years, which in New England are about eight years apart. All the young trees seen were growing in situations where at least fairly abundant light was available. It seems probable therefore that the white spruce is also largely dependent upon windfalls for its successful reproduction in the virgin forest. It is able to withstand severe winds without breaking, as is shown by individuals towering conspicuously above the general forest level. It is not particularly liable to fungus injury. Birth-rate and mortality are both low, and the species is able to maintain its small proportion in the forest.

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OTHER TREES.—*Pyrus americana* (Marsh) DC (mountain ash), though fairly common, is of little importance ecologically, since it is very short-lived, never reaches any great size, and produces little shade. Its life history in most respects is similar to that of the birch, and it has the same habit of producing sprouts from the stump. *Pinus Strobus* L. (white pine) is scattered thinly through many parts of the forest, generally towering high above the other trees. Its ecological status seems to be similar to that of the white spruce. There is no indication that in recent times at least it has ever been abundant upon Isle Royale. *Picea mariana* (Mill) BSP, *Larix laricina* (DuRoi) Koch, and *Populus tremuloides* Michx., which are found here and there in the climax forest, will be sufficiently treated in connection with quadrats 5 and 6. *Populus balsamifera* L. also occurs sparingly.

TAXUS CANADENSIS.—The most important of the lower plants of the forest—more important indeed than many of the trees—is the ground hemlock. Its influence lies in the completeness with which it occupies and shades the ground, preventing tree reproduction over large areas. This effect will be noted in connection with quadrats 5 and 6, and quadrat 1 includes part of a ground hemlock area in which trees are practically absent. *Taxus* can endure considerable shading, but is never found in the dense shade cast by the balsam groups. Balsam in its turn is excluded from large areas by *Taxus*, so that the competition between these two species is exceedingly keen. *Taxus* spreads abundantly by underground stems, and in this way invades new areas of forest when conditions are favorable, at the same time dying out in the older portions of the growth, thus allowing other plants to start in such places.

III. QUADRAT STUDIES

The method of investigation whereby a knowledge of the dynamics of the forest was gained was as follows. A rectangular area was laid off, made up of one or more units of 5 m. square, the usual size being a quadrat of 10 m. square, or four units. In the diagram of this area the position and kind of every tree, down to the smallest seedling, was plotted and its diameter noted. Cuts were next made with an ax to the centers of the large trees, and the small

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ones were felled. The age of every tree was then determined by counting the annual rings, and note was made in each case of the degree of soundness of wood, width of rings, and periods of suppression indicated thereby. The cuttings were made at the height of about 0.3 m. An element of error is introduced here, making the age as determined a few years too low. It seemed inadvisable, considering the many quadrats to be studied, to use up much valuable time in making the counts absolutely accurate. This would have involved the cutting of every tree at the surface of the ground, a very difficult and slow process. A saw might have been used instead of an ax, but when the rings are at all obscure it is impossible to count them from a sawed surface. I believe that the error introduced does not affect the validity of the results, since it is approximately the same in nearly every instance. The method on the whole gave excellent results, in the study of the rock shores and bogs as well as of the climax forest. Its use was made easy by the comparatively small size of the Isle Royale trees. Sixteen quadrats were studied in all, comprising 74 units of area, and involving the determination of the ages of about 900 trees. If objection be raised that the method is unduly destructive, it may be answered that the cutting over of these small areas produces exactly the same effect as does windfall, a process that is continually taking place, and thus makes possible a new crop.

In addition to the statistical study of the trees, careful notes were taken of the lower vegetation and the physical factors of the habitat. Less detailed studies of many other localities were also made for comparison with the quadrats.

The results of the quadrat studies so far as they concern the climax forest will now be given in detail. The first four described were located on Smithwick Island; quadrats 5 and 6 were upon the main Isle Royale.

Quadrats on Smithwick Island

QUADRAT 1 (fig. 6).—This quadrat exhibits most clearly the relations which the different tree species hold to each other and to the physical conditions of the habitat. It includes but one spruce, an aged giant 250 years old, long past maturity, with sparse foliage,

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giving practically no shade. Two healthy birches (105 and 107 years old), close together, produce considerable shade in their vicinity. There are several rather old balsams (64–90 years) well

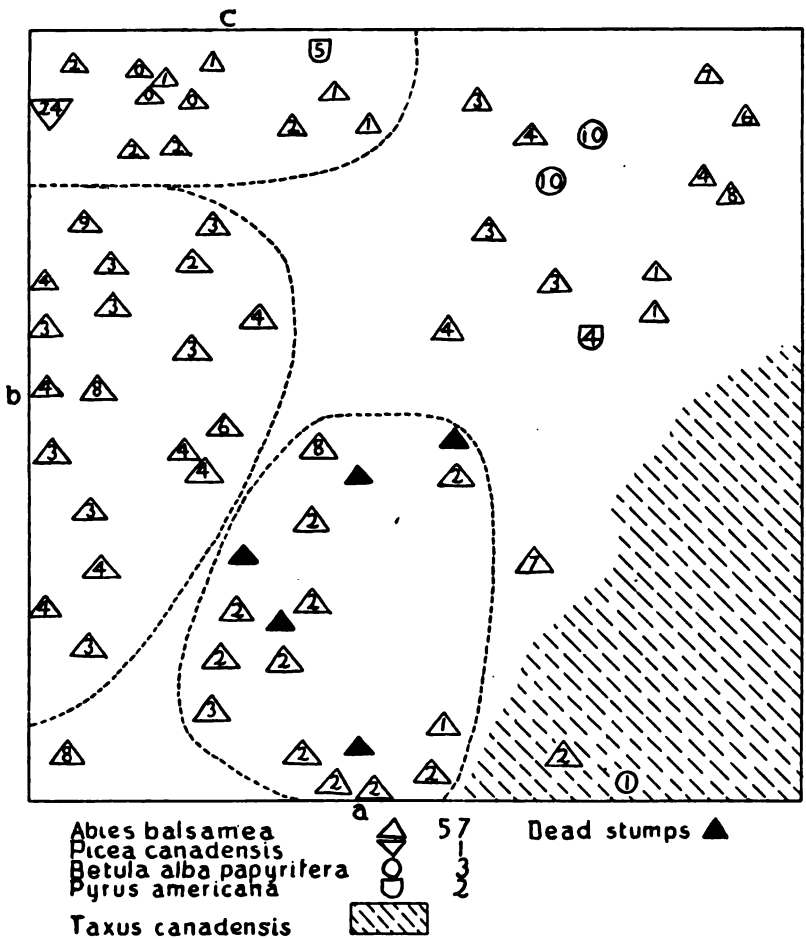

FIG. 6.—Quadrat 1, Smithwick Island: the symbols indicate the species; the numbers within them the ages of the trees by tens; for example, a tree marked *6* is between 61 and 70 years of age.

scattered over the quadrat, and usually more or less isolated from the smaller growth. The young trees are practically all balsams, the only representatives of other species being two mountain ash

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(one a clump of three stump sprouts) and a 20-year old birch in the lower right-hand corner. The young growth is not evenly distributed, but shows a tendency toward grouping, which tendency will be seen in each of the succeeding quadrats. The larger number of trees of each group are approximately even-aged. For example, the rather scattered group *a* that surrounds the 5 balsam stumps contains 13 balsams, 10 of which are 23–28 years old. Of the 18 trees in group *b*, 14 are between the ages of 30 and 50, not so uniform as the last, but decidedly of a single generation. Of the 13 trees in group *c*, all but the mountain ash and the large spruce are under 30 years.

Group *a* illustrates in a striking manner the way in which these even-aged clusters come into existence. Within its limits were 5 large rotten balsam stumps from which the trees had been broken a meter or more above the ground. The group evidently constitutes a windfall, probably caused by a single storm, one tree in its fall carrying others with it. Such windfalls of various ages are exceedingly numerous throughout the forest, the balsams, on account of their brittleness and susceptibility to fungus attack, being the ones most frequently destroyed. This particular windfall is of special interest because it was possible to determine the time at which it occurred. One of the large balsams in falling pinned to the ground a young tree of the same species, which, in spite of unnatural position and dense shade caused by the branches of the fallen one, has continued to live up to the present. The younger tree was 49 years old, and the first 12 rings were exceptionally wide, showing that up to the age of 12 years it was an unusually vigorous sapling. At this point a sudden change becomes evident, for the remaining rings are so close that in counting them a magnifying glass was an absolute necessity. This change could have been brought about only by some sudden and violent cause, and this cause is evidently to be found in the fall of the older tree. The windfall is therefore to be dated about 37 years ago. Returning to the trees composing group *a*, we find that they are all balsams; one is 85 years old, another 38, a third 14, and 10 range from 23 to 28; 11 then are subsequent to the windfall, and 10 began life

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within a period of six years, 9–14 years after the windfall occurred. There is only one that clearly antedates it.

Upon inquiring as to the cause of these facts, the factor of radiant energy immediately suggests itself (see p. 20). The older balsams, now fallen, when living were close enough to cast a dense shade over the area which they controlled, and there can have been no young trees beneath them, since if there had been, the present generation would antedate the windfall. It was not until 10 years after that event that young balsams began to appear in the area. Radiant energy being the principal factor involved, this interval of a number of years is entirely to be expected, since some time would elapse before the disintegration of the tangle of branches with their persistent needles would allow a large amount of the energy to reach the ground. Evidence in support of this hypothesis was found in every quadrat and in every considerable part of the forest. In no other case was it possible to determine the exact age of the windfall, but the general relation between the older and younger generation was usually plainly to be seen. Frequently the only sign of windfall is in the rotting moss-covered logs, but the close group of even-aged trees, sometimes 50 years old or more, tells the story plainly.

In quadrat 1 two other windfall areas are shown, one (*c*) quite recent, the other (*b*) older. The greater range of age among the trees in these areas suggests that those of the former generation did not all fall together. This type of windfall is commoner than that represented by group *a*. The fall of the first trees gives the wind a better chance to reach others. This slow process may be extended over a long period, even until the new generation has begun to fill in the gaps first made. In contrast to the dense grouping just described is the remaining area of the quadrat, where the individuals are less closely placed and are on the average much older. The part not included in the three groups comprises two-thirds of the area of the quadrat, yet it contains only 18 trees, 7 of which are over 60 years; while the other third of the quadrat contains 45, only 5 of them being over 60 years. The fewer trees in the larger part nevertheless produce a dense shade, and there is very little young growth beneath them.

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There is a difference that should be noted between the shade-producing capacity of the balsam and that of the birch. The former, with its many whorls of short branches close together and its opaque leaves, casts an exceedingly dense shadow which does not influence a large area. A moderately close stand of large balsams allows extremely little light to reach the ground. The birch (in its primeval forest form) influences a large area, but its shade is not dense, because of its comparatively thin crown and translucent leaves. Under the shade of large birches there is frequently a scattering of young growth, while under thrifty balsams there is rarely to be found any at all. Both conditions are well shown in the diagram of quadrat 1.

The effect of shading is seen also in the undergrowth. In the dense shadow of the balsams there is a mere sprinkling of herbs, and mosses are usually absent entirely, the ground being covered with a layer of tree waste. It is in shade of moderate density and in openings that the greatest luxuriance of mosses and herbs is found. The ground hemlock is excluded from most of the quadrat for the same reason, but in the lower right-hand corner there is an area completely occupied by a dense growth of it, which effectually prevents the establishment of any other species.

QUADRAT 2 (fig. 7).—This quadrat shows the same features as the last. Group *a* contains a great number of young trees of similar age, mostly balsams, which have started as a consequence of one or more windfalls. Of the 40 balsams in the area, 33 are between the ages of 20 and 35 years, and within these limits, as shown by the diagram, there is a tendency for those of similar age to be neighbors. Numerous fallen trunks represent the former generation. The large balsam marked "12," which was 121 years old—an unusual age for this species—was past maturity, and like the big spruce in the preceding quadrat was ineffective in producing shade. At *b* there is a part of an older group, 5 of the 7 balsams being between 44 and 53 years old. The upper left-hand corner is dominated by a few old and large trees, balsams and birches, with practically no young ones—only a few beneath the birches. The shade in this area was dense and the undergrowth sparse, even the ground

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hemlock being nearly absent. No spruce grew in this quadrat, but there were occasional large ones near.

QUADRAT 3 (fig. 8).—This small quadrat of one unit area shows a group of even-aged trees, among which are several young birch

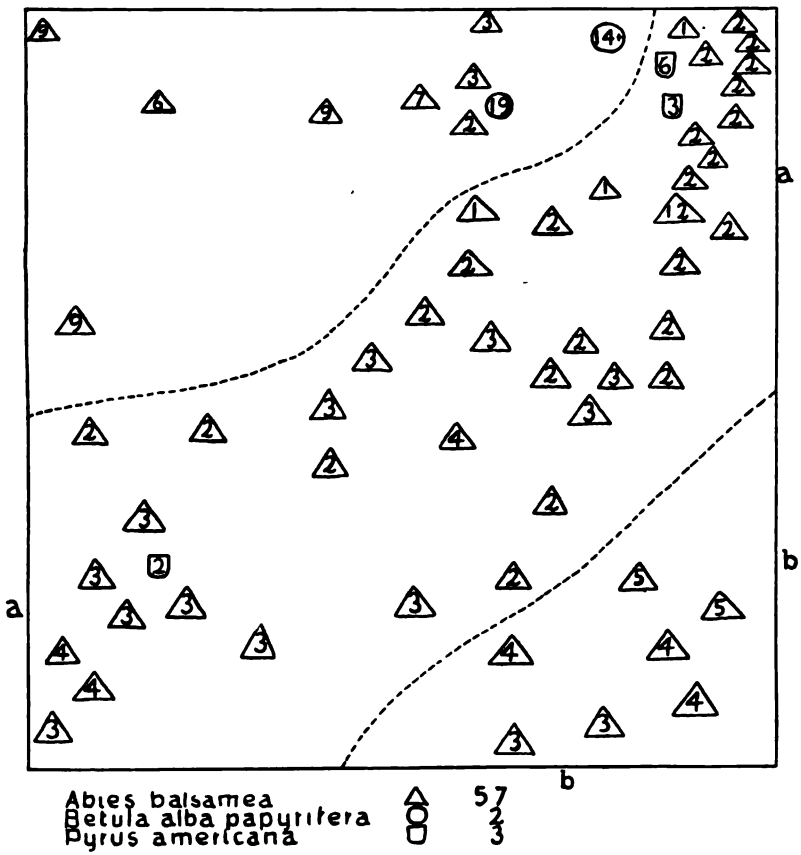

FIG. 7.—Quadrat 2, Smithwick Island; for explanation of symbols see fig. 6

and mountain ash as well as balsam. No living trees of a former generation are present within the limits of the quadrat, but several were seen near. Decayed trunks were frequent and were mostly birch. Of the 37 trees, 26 were within the ages of 26 and 35 years, and the others were very close to these limits. Evidently then all

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three species started growth at practically the same time, and the immediate cause was a windfall. The birches are tall and spindling, but now slightly overtop the balsams in spite of a somewhat later start. Having gained the advantage as to light supply, their tops will spread fast, and these trees, or more likely one or two of them, will doubtless finally develop the thick-stemmed, spreading, round-topped form characteristic of mature specimens in the virgin forest. The balsams which are within the sphere of influence of the birches will be suppressed. This process in fact has already begun. The last 5–10 rings of those balsams which were close to the birches were found to be noticeably narrower than the earlier ones, while the rings of those growing isolated from other trees were uniformly spaced. Undergrowth was practically lacking, the shade being everywhere very dense. Even the ground hemlock was entirely absent.

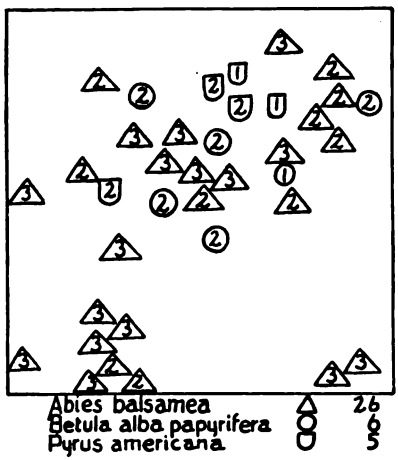

FIG. 8.—Quadrat 3, Smithwick Island; for explanation of symbols see fig. 6.

In this quadrat the mountain ash showed an interesting habit of growth. Several saplings were seen among the closest groups of balsams which were so slender and weak as to closely resemble lianes. One specimen was 4.3 m. high and 2.25 cm. thick at the base, unbranched, with a single tuft of leaves at the top. It was supported entirely by the balsams against which it leaned, and its upper portion had penetrated among the interlacing balsam branches close to the trunk of a near-by tree. It was 16 years old, and had evidently started before the balsams had begun to shade the ground thoroughly, but was left behind in the severe competition for the available light supply.

QUADRAT 4 (figs. 9, 10).—This quadrat, also of one unit area, includes two generations of balsam and no other species. Several large birches were near by and a large spruce. The older generation

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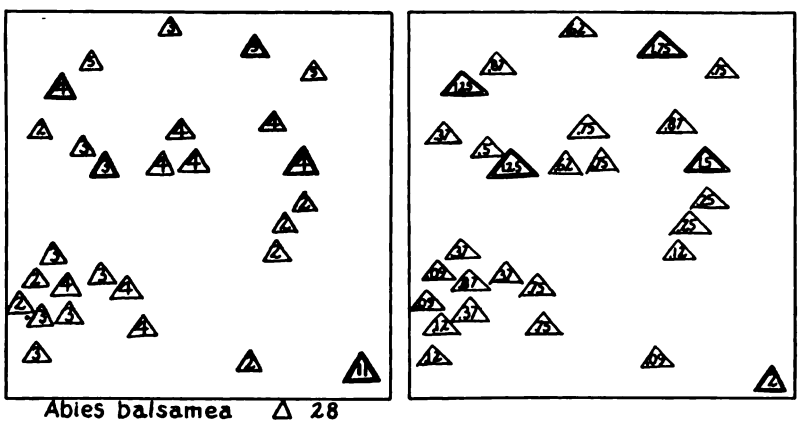
is represented by one individual in the lower right-hand corner, well isolated from other trees, 115 years old. The younger generation illustrates competition between individuals of a single species which began life at about the same time. Fig. 9 shows the age of each tree, and fig. 10 its diameter, which, it may be noted, maintains a pretty constant proportion to height. It will be seen from the latter that 4 trees (marked by double symbols) have attained a much greater size than the others; and if comparison be made with fig. 9 it will be evident that these 4 are not noticeably older than



FIGS. 9, 10.—Fig. 9, quadrat 4, Smithwick Island: age of trees; for explanation of symbols see fig. 6; fig. 10, quadrat 4, size of trees; the numbers indicate the diameters of the trees in decimeters.

their neighbors. The annual rings of these 4 trees were found in every case to be wide and evenly spaced, while those of their less favored companions were either very narrow from the beginning or plainly showed recent suppression. This illustrates an important principle in forest study, namely, that no reliance can be placed upon the size of a tree in fixing its age or in determining its place where two or more generations are concerned. These 4 individuals in some way gained the advantage early in life and caused the suppression of their neighbors. Evidence of the severity of the shading was shown by the presence among the living balsams of 20 dead specimens, averaging a meter in height, and in length of

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life from 14 to 38 years. Some had been dead for a long time, while others showed evidence, in needles still clinging, of having been alive until very recently. All had undergone severe suppression. In consequence of the deep shade the undergrowth was extremely sparse, except in the lower left-hand corner where there was a partial opening. Here was a luxuriant growth of mosses, including *Hylocomium proliferum* (dominant), *Hypnum crista-castrensis*, *Calliergon Schreberi*, and *Dicranum undulatum*. The close group of young balsams occupying this locality was largely due to layering. Quadrat 4 then includes in the main a group of balsams of very different sizes, giving an appearance of gradual reproduction, but in reality essentially even-aged, and belonging distinctly to a single generation.

Quadrats on the main Isle Royale

It has been said that the conditions on Smithwick Island include one that is somewhat abnormal for the region as a whole, namely, that the exposure to wind is greater. Two quadrats in sheltered localities on the mainland of Isle Royale were studied for the purpose of comparison. They probably represent the opposite extreme so far as exposure is concerned.

QUADRAT 5 (figs. 11, 12) was located a few hundred meters back from the southeast shore of the Blake Point peninsula in sec. 23, T. 67 N., R. 33 W. The locality is thoroughly sheltered from northwest winds by the main ridge, and from the lake winds by the islands to the southeast. On the diagram several points of difference from the preceding quadrats are readily seen. Most noticeable are the greater average age of all species and the absence of very young growth. Two new trees appear: *Picea mariana* (Mill) BSP (black spruce) and *Larix laricina* (DuRoi) Koch (tamarack), each species being represented by one individual. The whole stand is remarkably even-aged, 22 of the 38 trees being between the ages of 82 and 98 years. There is some tendency toward grouping of trees of similar age, though not so noticeably as on Smithwick Island. The group *a* is a very marked one, however. Of the 9 individuals of 4 species composing it, 7 are between 83 and 92 years, and 5 between 89 and 92. The effect of

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shelter from wind is very evident in the greater height of the trees. The protection which this area enjoys does not by any means prevent windfall, but merely lessens its intensity, and allows the trees to reach a greater height before they are overthrown. Several

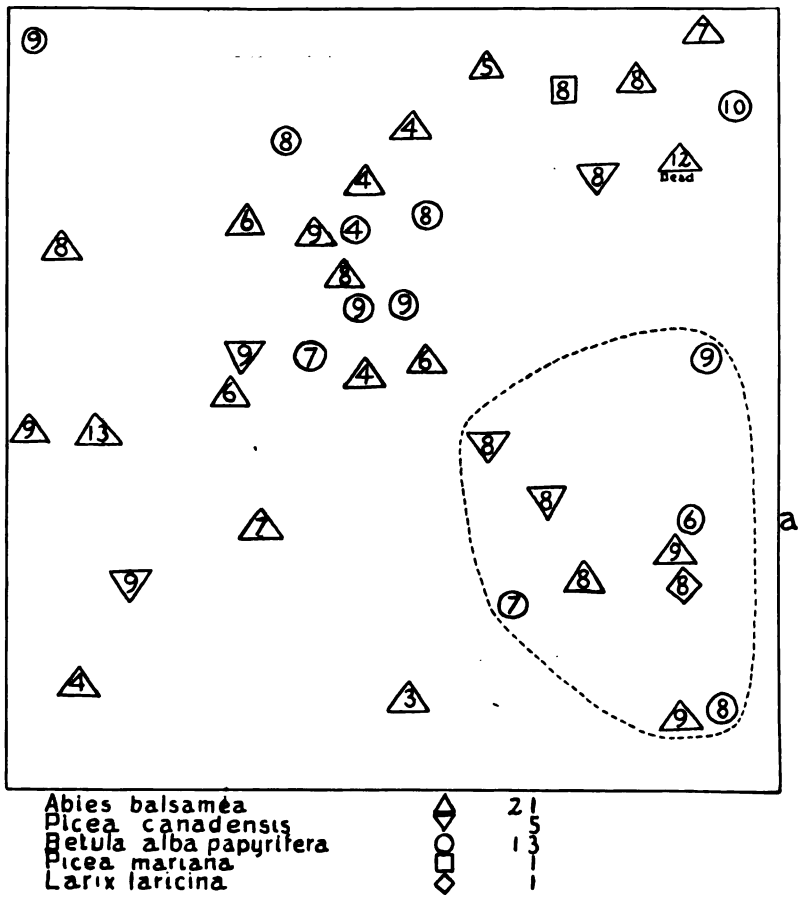

FIG. 11.—Quadrat 5, Blake Point Peninsula: age of trees; for explanation of symbols see fig. 6.

standing dead balsams were seen on this quadrat and they were frequent through the neighboring forest. On the outer islands the balsams almost never die a standing death. Quadrat 5 (fig. 12) also shows suppression of part of the stand, the larger trees being

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indicated by double symbols. The absence of very young growth is explained by the fact that the forest floor was covered by a thick mass of ground hemlock.

Black spruce and tamarack are found occasionally throughout the forest. Since they are both very intolerant of shade, they probably make a successful start only where an extensive windfall

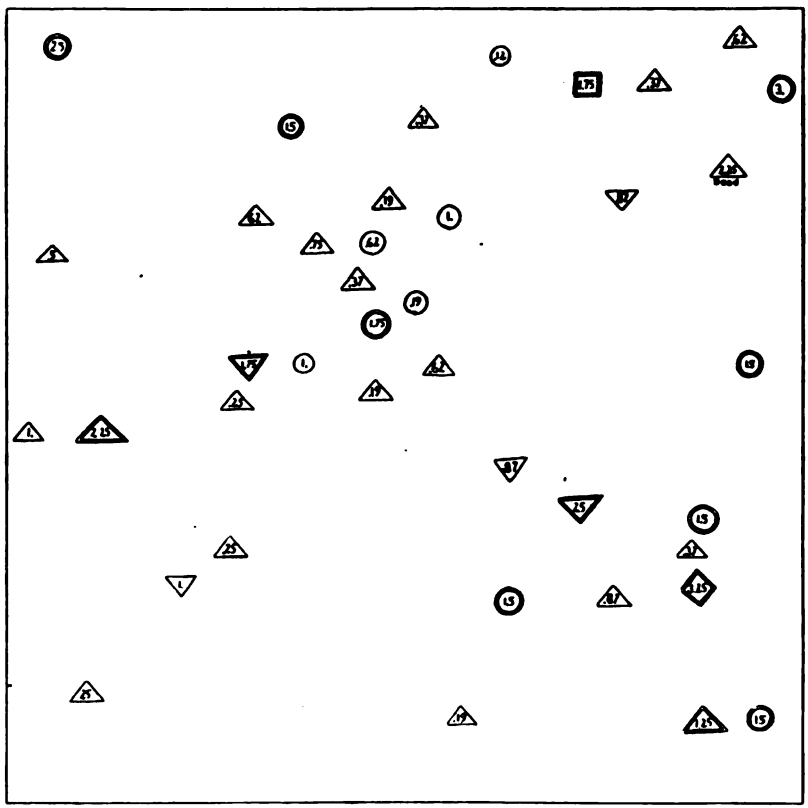

FIG. 12.—Quadrat 5: size of trees; for explanation of symbols see fig. 10

has let in abundant light. The black spruce as a member of the upland forest is abundant in one locality on the southeast shore of Isle Royale and in certain other places. The evidence seems to show that this species in abundance in the upland forest indicates a transitional stage approaching the climax. The subject will be treated again in the consideration of the rock shore succession.

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QUADRAT 6 (fig. 13).—The conditions here as to shelter were similar to those of the last. The quadrat was located near the shore of Tobin's Harbor in sec. 33, T. 67 N., R. 33 W. The small number and large size of the trees are noticeable, and also the entire

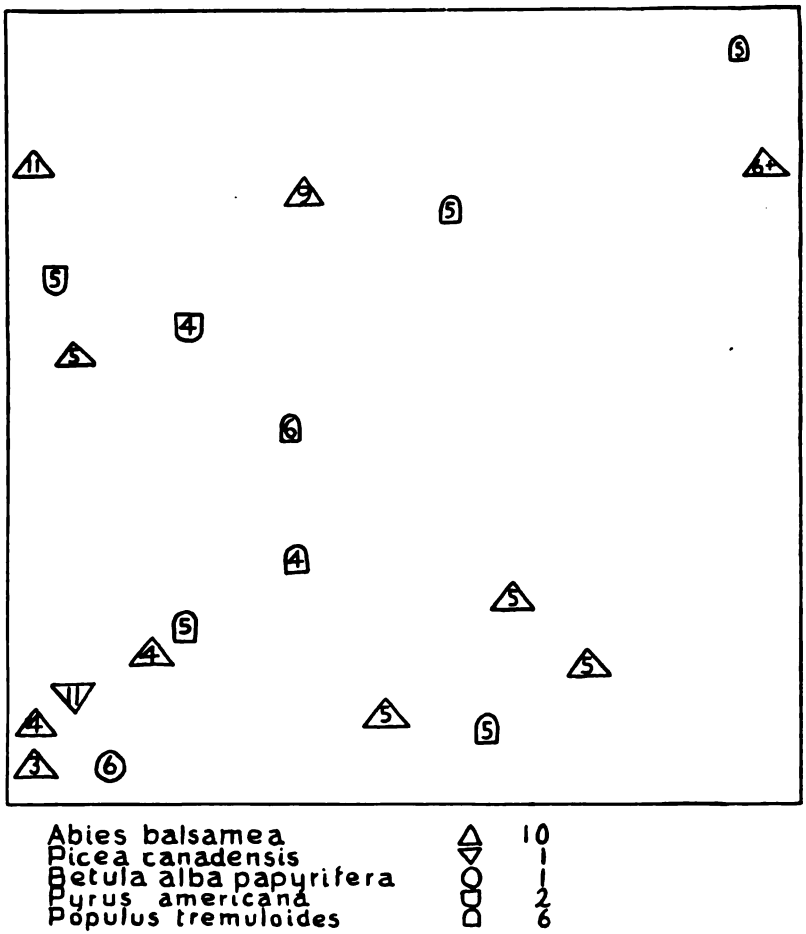

FIG. 13.—Quadrat 6, near Tobin's Harbor; for explanation of symbols see fig. 6

absence of young growth, in spite of the comparative lightness of the shade. These conditions were plainly due to the mat of ground hemlock which practically covered the quadrat. The ground hemlock therefore, rather than any tree species, dominates and

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controls this area. The surrounding forest was found to be essentially similar to the sample, except that the cover of ground hemlock was not continuous, and where it was absent the usual conditions of windfall reproduction, especially of balsam, prevailed. The large number of good-sized trees, balsams being specially noticeable, owe their continued existence to the protected position of the area. The presence of *Populus tremuloides* Michx. (aspen) in considerable abundance is noteworthy. This species seems to be ecologically equivalent to the birch, except that it does not to any great extent possess the power of sprouting from the stump, at least in this region.

A similar situation was noted in a narrow valley near Duncan Bay (sec. 28, T. 67 N., R. 33 W.), which was protected by abrupt ridges on both sides. Here the trees of all species are very large, the shade is not dense, and windfalls are relatively scarce. Ground hemlock is exceedingly abundant and large, and is plainly responsible for the lack of young tree growth and the resulting openness of the forest. Some scattered groups of small balsams were plainly related to windfalls.

The foregoing studies show that the climax forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little or no young growth beneath, those of a single group being approximately even-aged. This mosaic or patchwork changes continually in a manner that may almost be called kaleidoscopic when long periods of time are considered. The forest as a whole, however, remains the same, the changes in various parts balancing each other.

EXTENT OF THIS TYPE OF FOREST AS THE CLIMAX OUTSIDE OF ISLE ROYALE

Attempts to obtain information relating to the nature of the climax forest of other portions of the northeastern conifer region have not been attended with much success. The distributions of the various trees have been determined by BELL (8) and others with considerable accuracy, but practically nothing of an ecological nature has been published. From the data I have been able to

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discover, the impression has been gained that the same association of balsam, paper birch, and white spruce, which is the dominant forest type of Isle Royale, is found in the most mesophytic habitats throughout northeastern Canada. The probability is that it is the climax type over much of the region, though there is not sufficient evidence to justify a confident statement to that effect. It is not necessary that the component species bear the same relations to each other in all parts of the region, or even that the species themselves be everywhere the same. One or even two of the climax trees may be lacking in certain places, species that are ecologically equivalent may be substituted, or others added. Analogous differences occur in the deciduous forest. The two climax trees that are almost omnipresent are the maple and the beech, and yet there is a belt along the northern edge of the region where the maple alone forms the climax forest, unless the yellow birch (*Betula lutea*) may possibly take the place of the beech. Again, in the Great Lakes region a third climax tree, the hemlock (*Thuja canadensis*) is present; and in the southern Appalachians the number of species composing the climax forest reaches a dozen or more. Similarly, in northeastern Canada the climax forest may vary from place to place.

Of northern Quebec MACOUN (**39**) says: "In the country around Lake Mistassini it [balsam] grows mixed with aspen, birch, and white spruce, and on the lower part of the Rupert River it is found growing with the same trees all the way to James Bay." The correspondence of this to the Isle Royale forest is striking. In reports of the Department of Lands and Forests of Quebec (**45, 46**) expressions such as the following are frequent, the region described being the country north of Lake St. John, west to Lake Abitibi: "well timbered, mostly with spruce, fir, and white birch, with some scattered white and Banksian pine on the high ridges." In the "Report of the survey and exploration of northern Ontario" (**43**) there is much detailed information concerning the distribution of the trees in that region, though the data presented have little ecological value. However, in reading the reports of the various parties one frequently comes upon such statements as the following: "chiefly small poplar [*Populus tremuloides*], spruce, white birch,

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and balsam, and a few balm of Gilead [*Populus balsamifera*]"; "spruce, balm of Gilead, poplar, balsam, and white birch"; "white birch, balsam, and a few large spruce"; "the white variety of spruce of good size was seen continually along the rivers and on

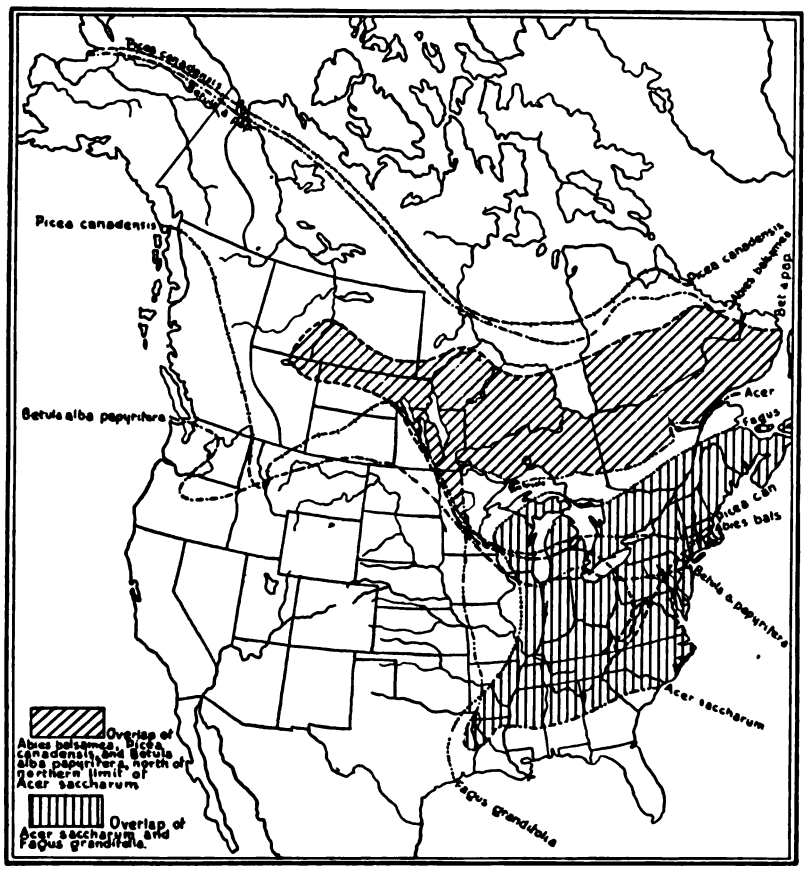

FIG. 14.—Ranges of the climax trees of the northeastern conifer forest and the eastern deciduous forest.

ridges back from them. Black spruce, generally scrubby, clothes the muskegs. . . . . Birch and balsam are also common on high lands." The black and white spruces are not usually distinguished in these reports, but it is clear that the former is the principal tree upon the extensive muskeg lands, while the latter is confined to the

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higher grounds, where it usually has the balsam and birch as its companions.

The data here presented, though very unsatisfactory, are sufficient in my opinion to establish the probability of the generalization that the climax type of the whole of the northeastern conifer region is of the general character described for Isle Royale, with local variations due to the elimination or addition of species, or to the substitution of others that are ecological equivalents.

Important confirmation has recently been received from Dr. ROBERT BELL of Ottawa, the best authority upon the distribution of Canadian trees, who writes: "The same type of upland forest which you describe on Isle Royale extends from the Great Lakes to James Bay and east and west of it, with modifications in parts."

On the map (fig. 14) the area shaded with oblique lines represents the region over which the ranges of the balsam, paper birch, and white spruce overlap, *north* of the range of the sugar maple (data largely from TRANSEAU **55**). It is in this region that the type of forest described is thought to be the climax. Beyond the limits of the balsam, which has the narrowest range of the three, some other species must be substituted for it, or else the climax forest is composed of the remaining two species alone.

COMPARISON WITH THE CONIFER FOREST OF THE SOUTHERN APPALACHIAN SUMMITS

In connection with the study of the Isle Royale forest it will be worth while to make comparison with another region that has come under my observation, where the forest is extremely similar to that described in the present paper. On the highest summits of the mountains of North Carolina, eastern Tennessee, and southwestern Virginia, there are isolated areas of dominantly coniferous forest, which seem like detached portions of the great northeastern forest (see detailed description by HARSHBERGER **32**). The species are different, the balsam being *Abies Fraseri* (Pursh) Poir., the spruce *Picea rubra* (DuRoi) Dietr., and the birch *Betula lutea* Michx. f. In general aspect this forest is surprisingly like that of Isle Royale. Because of the predominance of the first tree mentioned many of the mountains themselves are locally called "Bal-

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sams." The results of studies upon three of these summits in western North Carolina may be briefly summarized as follows, the localities being Richland Balsam, Plott Balsam, and the Black Mountains (Mount Mitchell).

The coniferous forest covers the mountain slopes from about 1600 m. to the summits, the highest of which is about 2010 m. *Abies Fraseri* is on the whole the most abundant species except along the lower edge of the coniferous region, where *Picea rubra* is of somewhat greater importance. *Betula lutea* is scattered more or less thickly throughout and grows to a great size, specimens having been noted that were 1.3 m. in diameter. As on Isle Royale, birch and spruce are sparsely represented in the young growth, which is predominantly balsam. The shrubby vegetation consists almost entirely of *Rhododendron catawbiense* Michx., which is very abundant. It is interesting to note that the balsam seedlings are practically absent under the shade of the rhododendrons, and scarce in shade in general, but are exceedingly abundant in partial openings. The ground is covered by a luxuriant moss carpet, almost identical in composition with that of the Isle Royale forest, and the herbaceous growth includes most of the characteristic group of northern forest plants which has been listed (p. 16).

The similarity between Isle Royale and the North Carolina "Balsams" is thus a striking one. In the latter region there is even an ecological equivalent to the ground hemlock. *Rhododendron catawbiense*, in spite of its very different habit, is equally effective in densely occupying and shading the ground and thus in temporarily preventing reproduction of the forest trees over wide areas. I believe that the conclusions which have been reached concerning the Isle Royale forest will also hold, with minor modifications, for the forests of the North Carolina summits. The conifer-birch forest of the mountains is to be regarded as the climax type of its own limited area (not including, of course, the lower slopes dominated by deciduous trees), and at the same time as an extension or outlier of the northeastern climax forest.

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THE MAPLE FOREST OF ISLE ROYALE AND ITS RELATIONS

Wherever the sugar maple occurs it forms a part of the climax forest, and is usually the dominant species therein. Between the two great eastern forest regions there is a transitional belt several hundred kilometers wide where the three climax trees of the conifer, and the two of the deciduous forest all occur (see map, fig. 14). This belt extends from northern Wisconsin through the upper peninsula and the northern part of the southern peninsula of Michigan and eastward to New Brunswick. WHITFORD (**59**) studied the successions in a portion of this belt, and found that the climax forest in northern Michigan (both peninsulas) is the beech-maple type. The balsam, birch, and spruce are very abundant, but here they belong to preliminary stages in the successions. GANONG (**26, 27**) gives an excellent summary of the plant formations of New Brunswick. He states that the climatic forest type is the "mixed maple-birch-spruce-fir association." There is no indication in his paper that the maple ever supersedes the other trees, but the presence of such a possibility must be admitted. The conclusion from the studies of WHITFORD and others seems to be that the maple and beech, where not climatically excluded, are able to supersede the climax trees of the northeastern forest.

Coming now to Isle Royale, we find upon the southwestern end, occupying the summit of the highest ridge, a mixed growth of *Acer saccharum* Marsh (sugar maple), *Betula lutea* Michx. f. (yellow birch), and *B. lenta* L. (sweet birch); with the characteristically northern trees as a minor element (see ADAMS **4**, pp. 30–31, and HOLT **33**, p. 224). The maple is decidedly the dominant species and reaches a large size.[1] At the northern edge of this northernmost outpost of the maples we may draw the line that separates the true northern forest from the transitional belt (fig. 14). South of this line the representatives of the southeastern deciduous forest, though not necessarily forming the bulk of the stand, yet have the upper hand; north of it the supremacy of the conifers and the paper birch is undisputed.

[1] It is of interest to note that the maple is common on the southern side of Michipicoten Island, near the eastern shore of Lake Superior.

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Since glacial times there has been a continual northward advance of the forest, with the conifers as the pioneers, closely followed by the hardwoods. The problem as to whether the extension of the latter is still going on might be studied to good advantage in such localities as the southwestern end of Isle Royale, and Michipicoten Island. The large size and thriftiness of the maple at its northernmost limit would seem to indicate that it has not reached its climatic limit (BELL 8). The manner and causes of "climatic successions," or the invasion of one climax forest by another, are still to be worked out.

SUMMARY.—THE CLIMAX FOREST

I. The dominant forest of Isle Royale is composed of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*, with a few other species occasionally present. *Abies*, all sizes and ages considered, is by far the most abundant, but the greater number of individuals are small. *Betula*, although conspicuous, is not abundant, and young trees are scarce. *Picea* is rare, though occasional specimens tower high above the other trees. Shrubs and herbaceous growth are sparse except in partial openings. The most important element in the latter is the moss contingent, which is responsible for the formation of great amounts of humus.

II. Studies of individual species gave the following results. *Abies* is preponderant in the young growth because (1) the seedlings make a successful start in almost any situation provided sufficient light be available; (2) the species reproduces abundantly by layering. Its rapid decrease when greater size and age are considered is due to (1) competition because of abundant germination; (2) fungus attacks, and (3) brittleness of wood, both resulting in extreme liability to windfall. Its high birth-rate is balanced by a high rate of mortality. *Betula* does not germinate abundantly in the forest, but, because it is not liable to disease and windfall, holds its own with *Abies*. Even when broken off by severe winds it has a means of recovery in its ability to produce stump sprouts. Its more rapid growth gives it an advantage in competition with *Abies*. Abundant light is necessary for successful reproduction. Low birth-rate is compensated by a very low mortality. *Picea* is

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ecologically unimportant on account of its scarcity. Germination in the forest is less abundant than in the case of *Betula*. It is not liable to fungus attacks and withstands severe winds. Birth-rate and mortality are both low. *Taxus canadensis* is the most important species of the undergrowth, its influence lying in the completeness with which it occupies and shades the ground, preventing tree reproduction over large areas.

III. Intensive study of selected areas (quadrats) yielded the following facts concerning the dynamics of the forest.

The forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little young growth beneath. The history of a windfall area is as follows. After the débris has disintegrated sufficiently to allow abundant light to reach the ground, a new generation of trees springs up, approximately even-aged, composed of the three dominant species, *Abies* always greatly preponderant. During the continued development of this group most of the individuals are at various times eliminated, *Abies* suffering most for the causes enumerated in section II. Because of the dense shade no new individuals can start beneath them, and the final outcome is a group composed of a few large trees, approximately even-aged, in which *Abies* has nearly or quite lost its position of dominance to *Betula*. In situations sheltered from wind all species live to a greater age and windfalls are less frequent. The processes though less rapid are nevertheless the same as in more exposed situations. The result in the forest in general is a mosaic or patchwork which is in a state of continual change. The forest as a whole remains the same, the changes in various parts balancing each other.

IV. The following evidences that the dominant forest of Isle Royale is also the climax have been derived from the studies summarized above and from those dealing with the successions.

1. The dominant forest is the most mesophytic of the plant societies.

2. It is uniform upon all soils and upon areas that have passed through very different lengths of subaerial history.

3. All the successions culminate in the establishment of this as the final stage.

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4. The character of the forest as a whole is stable, though any given area is continually changing in composition and relative proportions of the various species.

V. The same type of forest, with local differences in some places, is probably the climax throughout the northeastern conifer region.

VI. Comparison with the conifer-birch forest of the southern Appalachian summits shows a striking equivalence of species and marked correspondence between the two in ecological characteristics, indicating that the forest dynamics are essentially the same. The mountain forest may logically be considered as a southward extension or outlier of the northeastern climax forest.

VII. *Acer saccharum* is dominant upon the main ridge at the southwestern end of Isle Royale, reaching here its extreme northern limit in this region. Southward it is probably able to supersede the conifers and birch, while north of its northern limit the supremacy of the latter trees is undisputed.

PALO ALTO, CALIFORNIA

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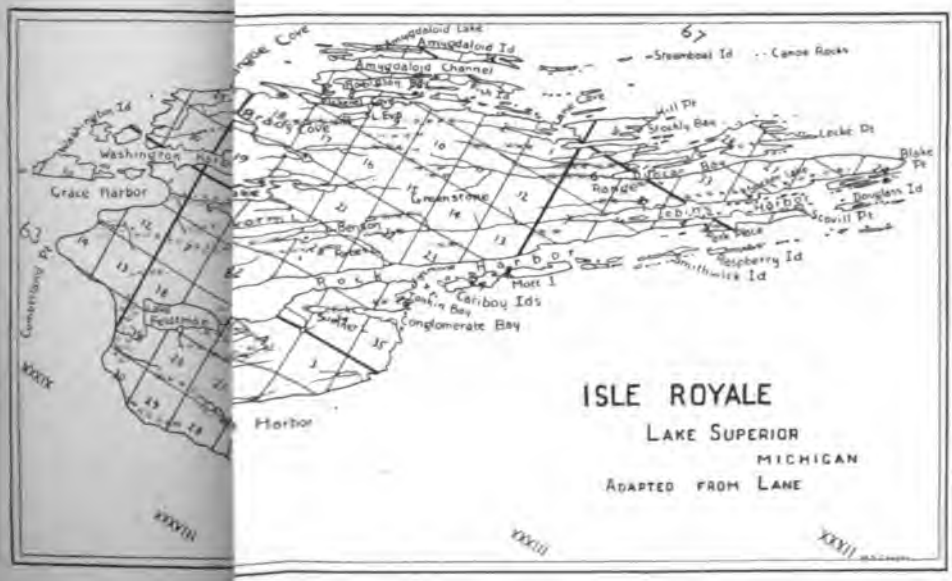

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PROGRESSIVE AND RETROGRESSIVE CHANGES IN THE PLANT ASSOCIATIONS OF THE DELAWARE COAST

LAETITIA M. SNOW

(WITH SIX FIGURES)

During July and August 1901, certain observations were made on the plant associations of the Delaware coast, from Cape Henlopen southward, for about six miles.[1] Ten years later, in July 1911, the same region was again visited in order to ascertain the changes which had occurred during the interim.

Considering the extreme instability of dune topography, surprisingly little change was noted, thus indicating the slowness with which plant associations, in general, change their character. Certain observations, however, seem of value, as indicating the direction of change in various associations, and are therefore recorded.

As in the previous study, on account of the lack of flowers and fruit, the identity of many forms was difficult—at times impossible—to determine. For regions which showed practically no change, no lists are presented. Where changes were noted, only dominant forms are given, in order that an idea of the direction of change may be obtained. The nomenclature of GRAY'S *Manual* (7th edition) is used, with the BRITTON synonyms in parentheses.

Grateful acknowledgment is due Professor KARL M. WIEGAND for his kind assistance in the identification of certain species.

I. Geography and physiography

As a general discussion of the position, topography, soil, and climate of the region was presented in the former paper, a consideration of these points will be omitted.

II. Plant formations

A. TREELESS OPEN

1. *Beach formation.*—(*a*) *Lower beach.*—The contour of the lower beach varied exceedingly during July 1911, thus indicating

[1] SNOW, L. M., Some notes on the ecology of the Delaware coast. BOT. GAZ. 34:284–306. *map* and *figs. 1–10.* 1902.

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an unstable condition. This instability is further evidenced by the fact that, during the 20–25 years which have elapsed since some of the summer residents first visited the region, the beach and the sea-cliff, along which Surf Avenue extends, have receded many feet. After great storms, especially during the winter, the beach is said to be several feet lower, exposing at such times ledges of peaty material. During the period of this study one small ledge nearly in front of Hotel Henlopen, Rehoboth, was twice exposed,

FIG. 1.—Ledge of peat in the beach near Henlopen Hotel, Rehoboth, Del.

appearing somewhat as in fig. 1. It is said to underlie the coast from Rehoboth to the Henlopen Life Saving Station. One fisherman reported that in winter a ridge of "turf with stumps in it" is exposed in the beach opposite Delaware Avenue. Reference to similar beach-buried peat is made in the report of the Intercollegiate Geological Excursion, 1911.[2]

b) Middle and upper beaches.—As was noted in the former paper, no upper beach can be distinguished. This year there is

[2] The Intercollegiate Geological Excursion. Science N.S. 34:611–614. 1911.

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pratically no middle beach, the summer storm-tides usually reaching the bases of the frontal dunes. The succulents characteristic of this zone appear, therefore, around the bases and on the slopes of these dunes.

2. *Dunes.—Outer series.*—This series is practically fixed from the Henlopen Life Saving Station to a similar station at Dewey Beach, a distance of five miles. The dunes are held chiefly by *Ammophila arenaria*, with a sprinkling of *Cenchrus tribuloides* and succulents.

Between these dunes are many passages leading into hollows or lakes which are flooded in times of storm. As the beach is narrowing, the flooding of these regions occurs more frequently than formerly, thus causing a retrogression toward more hydrophytic conditions.[3] The best example of this is the "flooded area" north of Rehoboth, called in the previous paper "desert waste," because a large portion of it was at that time bare, damp soil. It is reported to be at times "dry with a shining crust," but in July 1911, although the month was a rather dry one, the whole area appeared to be under water, thus indicating a greater inflow from the sea. At the south edge of this region are to be found isolated plants of *Mollugo verticillata*, *Sesuvium maritimum*, and *Spergularia marina* (*Tissa marina*). A second example of flooding by the sea is presented by Silver Lake, south of Rehoboth. The presence of numbers of crabs in this lake indicates frequent additions of salt water. This inflow of the sea takes place at a point near the south end of the lake where the margin closely approaches the tide line. Similar retrogressive movements have been described by HARSHBERGER as occurring in northern New Jersey.[4]

As was formerly noted, a region of great activity extends from a short distance south of the Henlopen Life Saving Station to the Henlopen Lighthouse. The large dunes, forming three amphitheaters opening seaward, have moved many feet inland during the last ten years. In passing back over alternating pine ridges and swamps, they have exposed "pine graveyards" and left in

[3] COWLES, H. C., The causes of vegetative cycles. BOT. GAZ. 51:161–183. 1911.

[4] HARSHBERGER, J. W., The vegetation of salt marshes, and of salt and fresh-water ponds of Northern Coastal New Jersey. Proc. Acad. Nat. Sci. Phila. 1909:373–400. *figs. 1–6.*

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their seaward hollows swamps and ponds, which are at times flooded by the tide. In the third of these amphitheaters (fig. 2) many slabs of peat may be seen, which have probably been washed inland from the ledge below tide line.

Across the cape extends the long dune upon which stands the Henlopen Light. This is the largest dune in the region, estimated ten years ago to be 80–90 ft., when the crest was at the lighthouse. By 1911 the summit had moved about 300 ft. to the southwest, and

FIG. 2.—View from the crest of the lighthouse dune, looking south over the third amphitheater; flooded area in the distance.

appeared to be several feet higher than the base of the lighthouse. This advance has not changed the general appearance of the region, as photographs taken from the same points on both visits are very nearly identical. In spite of the fact that this is an active dune, a small clump of *Ammophila* has managed to gain a foothold on the crest (fig. 4).

The appearance of the cape after ten years is apparently unchanged. A low beach extends around the point, bordered on the inner side by low dunes, which inclose a complex of dunes and

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swamps. A few shrubs appear on the dunes and a low ridge bearing small trees nearly crosses the cape, as may be seen in fig. 5.

South of Rehoboth the edge of the frontal ridge of dunes passes into a rolling plain called "a heath," and, although the growth of the shrubs and stunted trees gives the region a more thicket-like appearance, the flora has apparently not materially changed.

3. *Hudsonia complex.*—North of Rehoboth may still be found the region called a "*Hudsonia* complex," a jumble of small dunes,

FIG. 3.—Eroded face of the lighthouse dune; view taken from the northeast slope.

held principally by *Hudsonia tomentosa*, with swamps occupying the depressions between them. The flora of these dunes exhibits a more heathlike character than it showed ten years ago. South of Rehoboth the drying of the *Hudsonia* complex has progressed still farther. Swamps are rather rare, remnants showing in places, where *Scirpus americanus*(?) and *Juncus* sp. give evidence of former swampy conditions.

4. *Swamps and meadows.*—As the flora around Silver Lake was studied somewhat more in detail ten years ago than that of the

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other meadows, it would have been interesting to have made careful comparisons this year. But unfortunately that region has been converted into a pasture, and is closely grazed. The few forms found in the fence corners, however, indicate an assemblage similar to that occupying this region ten years ago. As one passes northward the flora changes, many more heath forms appearing this year than at the time of the previous study. This seems to indicate that the higher land has become drier, while the land in lower

FIG. 4.—View from the top of the lighthouse looking southwest; this figure is a continuation to the right of fig. 2.

situations has maintained its swampy meadow character, due to the frequent additions of sea water to the lake.

North of Rehoboth, around Frazer's Lake, there extends a large swamp. Near the lake the cat-tail is apparently the dominant form, while to the east and north this association passes into a meadow which is a second pasture. This swampy meadow extends to the flooded area on the north and has a very uniform appearance. Only the southeastern extension, as it runs between the *Hudsonia* dunes, was studied. Many typical undrained swamp forms were

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DUNE

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folia have disappeared; while *Lyonia ligustrum* (*Xolisma ligustrum*), *Ascyrum hypericoides*, *Eupatorium hyssopifolium*, *Rubus* sp., *Vaccinium atrococcum*, *Gaylussacia baccata* (*G. resinosa*), *Baptisia tinctoria*, *Rhus Toxicodendron* (*R. radicans*), and *Quercus marylandica* have established themselves.

No sphagnum has been found, and none could be identified in the peat collected. The absence of typical peat bogs from the eastern shore of Maryland was noted by SHREVE,[5] although sphagnum was found abundantly in the clay upland swamps.

Hibiscus Moscheutos has apparently disappeared from these hollows in the ten-year interval, but whether this is due to the stress of changing ecological conditions or to the assiduous gathering of the plants cannot be stated.

5. *Heath.*—This formation shows a progression toward the development of a forest by a greater growth of the shrubs and trees, without much change from a floristic standpoint.

B. WOODED REGION

The thicket and forest formations have received no detailed study at either time, but the collections made this year indicate that the pine stage, represented by *Pinus Taeda* and *P. rigida*, is being succeeded by the oak-hickory stage, represented by young plants of *Quercus marylandica*, *Q. alba*, *Q. velutina*, *Q. stellata* (*Q. minor*), *Q. falcata* (*Q. digitata*), *Carya glabra* (*Hicoria glabra*), and *C. alba* (*H. alba*). The list of associated forms is incomplete, but it is interesting to note that the species found are not those characteristic of similar situations in New Jersey or southward,[6] but that many of the plants found in clay and sandy loam areas of the Talbot terrace of Maryland are present (SHREVE *loc. cit.*). According to the manuals, the northern limit of *Myrica cerifera*, a typical pine barren plant, is Maryland. It was found, however, at Rehoboth and is mentioned by STONE[7] as occurring in the southern

[5] SHREVE, F., The plant life of Maryland. Md. Weather Service, Spec. Publ. III. 1910.

[6] HARPER, R. M., Science 25:539–541. 1907.

[7] STONE, WITMER, The plants of southern New Jersey. Rep. N.J. State Museum. 1910.

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part of New Jersey. I agree with STONE (*loc. cit.*), SHREVE (*loc. cit.*), HARPER,[8] and WILLIAMSON[9] that the flora of southeastern Delaware has affinities, southward and northward, with districts much farther inland, rather than with the coastal regions.

C. THE CANAL DUNE

This dune, mentioned in the previous paper as having been formed, about a mile inland, from material excavated in making a canal, is at this time practically fixed. This is due (1) to the fact that the finer sand has been blown away, leaving the coarser material, and (2) to the binding power of plants. No *Ammophila* is to be found, but many of the plants characteristic of the *Hudsonia* complex and of the heath are present.

III. Problems connected with the region

Second series of dunes.—This series was omitted from the foregoing discussion, because of its possible relation to the problem concerning the change in direction of the coast line.

This ridge of dunes is best seen north of Rehoboth, extending to the northwest from the end of the board walk, thus making an angle with the coast. It was considered in the previous report (p. 286) to be a ridge of dunes blown from the coast in a southwesterly direction. The dunes lie on a hard, flat foundation of clay and sand impregnated with iron. This is continuous with the bluff along which Surf Avenue lies and with the clay-sand ledge south of the town, shown in fig. 6. A portion of this ledge was figured in the previous paper (p. 285) and erroneously called sandstone. At Dewey Beach there again appears a clay-sand ledge, crowned with dunes, which, taken in connection with the clay areas north of Silver Lake, may be a continuation of the same formation. In the absence of any geological information on the subject, the fact that these various outcroppings appear to be at the same level, together with their probable connection, suggests the possibility that this low bluff was the original sea-cliff, running from

[8] HARPER, R. M., Car-window notes on the vegetation of the Delaware peninsula and southern Virginia. Torreya 9: 217–226. 1909.

[9] WILLIAMSON, C. S., Notes on the flora of central and southern Delaware. Torreya 9: 160–166. 1909.

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Dewey Beach to Rehoboth roughly parallel with the present coast, and north of Rehoboth extending in a northwesterly direction. There are many irregularities in this line, now occupied by lakes, streams, and marshes, which suggest erosion of the cliff.

The second interesting problem is connected with the plant remains, which in a thick peaty mass apparently underlie a large part of the present beach. This deposit was undoubtedly formed in a swamp, which would indicate that at one time the coast line

FIG. 6.—Clay-sand ledge south of Rehoboth, Del.; view from near the end of the board walk looking south; Dewey Beach in the distance.

was *farther out*. The following history seems reasonable and is suggested as a possible explanation. The sea-cliff stage was followed by the formation of a bar to seaward, inclosing a lagoon, which by progressive changes became a swamp. That the swamp stage must have continued for some time is suggested by the report of "stumps in the turf." Erosion of the seaward side of the bar followed, involving the driving backward of the dunes over the swamp and the formation of a hook at the north end of the bar,

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thus extending the coast northward with the development of Cape Henlopen. This erosion stage is still in progress.

IV. Summary

1. Ten years is too brief a period in which to show any considerable change in plant associations, even in so active a region as that of the dunes.

2. Progressive changes were observed: (a) advancement of the *Hudsonia* complex toward the heath; (b) advancement of the heath toward the thicket; (c) drying of isolated swamps and lakes; (d) fixation of the "canal dune."

3. Retrogressive changes were noted: (a) recession of the coast, resulting in more frequent flooding of certain regions, thus continuing or increasing their hydrophytic character; (b) movement of active dunes over the forest.

4. The character and position of the sand-clay ledge suggests that it may have been an ancient sea-cliff.

5. The presence of a ledge of peat in the beach indicates the location of a former swamp.

6. This swamp was probably due to the presence of an ancient bar inclosing a lagoon.

7. The present erosion of the coast indicates that this bar with its dunes was moved inland over the swamp, while portions of the beach material were carried northward to form the hook.

8. This process of erosion is still in progress.

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RAY TRACHEIDS IN THE CONIFERALES[1]

RUTH HOLDEN

(WITH PLATES I AND II)

In classifying the various families of conifers from an anatomical standpoint, the structure of the medullary rays, whether fusiform or linear, thin or thick-walled, pitted or unpitted, has been a valuable criterion. Another feature which has not been emphasized as much as it deserves is the presence or absence of ray tracheids. DEBARY, MAYR, PENHALLOW, and others have reported them in certain genera, but to reach any conclusion of phylogenetic importance it will be necessary to consider the conditions affecting their appearance in all the main groups of conifers, extinct as well as living.

Extinct conifers

Succiniferous *Pityoxyla* of the Lower Cretaceous as described by JEFFREY and CHRYSLER (1) lack ray tracheids of any sort. In another less ancient cretaceous *Pityoxylon*, described by BAILEY (2), however, ray tracheids are present, both marginal and interspersed. Likewise in amber containing *Pityoxyla* from the Baltic deposits of the Late Eocene or Early Oligocene (3), marginal tracheids are present in the mature wood, though not in the early annual rings. In other types of fossil wood, namely *Cupressinoxylon*, *Cedroxylon*, *Taxoxylon*, *Araucarioxylon*, etc., ray tracheids have not been described.

Living conifers

ABIETINEAE

JEFFREY (4) has divided the Abietineae into two groups: the Pineae (*Pinus*, *Picea*, *Larix*, and *Pseudotsuga*) and the Abieteae (*Abies*, *Cedrus*, *Tsuga*, and *Pseudolarix*). Ray tracheids are present normally in all four genera of the Pineae, attaining their greatest complication in the hard pines, where they are dentate and reticu-

[1] Contributions from the Phanerogamic Laboratories of Harvard University. No. 48.

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late. Of the Abieteae, ray tracheids are present normally in *Cedrus* and *Tsuga*. DEBARY (5) and PENHALLOW (6) have both described them as characteristic of *Abies balsamea*, to which DEBARY adds *A. excelsa*, but as lacking in other species of *Abies*. More recently THOMPSON has investigated this genus (7) and found them absent invariably in normal wood, but recalled in a number of species as a result of injury. Curiously, he reports them lacking in *A. balsamea*, an observation which I have confirmed from a study of seedling, mature wood, vigorous branches, roots, cone axes, etc., wounded and unwounded. In *Pseudolarix*, also, I have been unable to find ray tracheids, even in severely wounded branches. *Pseudolarix*, however, seems to be a particularly unfavorable subject for the study of experimental morphology, traumatic resin canals being formed much less readily here than in the other members of the Abietineae. The only remaining genus, *Keteleeria*, has the wood structure of *Abies*. Ray tracheids are entirely absent even in such primitive regions as the first annual ring, cone-bearing branch, cone axis, and are not recalled after wounding, though there is an abundant formation of traumatic resin canals.

TAXODINEAE

The Taxodineae as a whole are simpler in wood structure than the Abietineae. The resin canals of the latter have disappeared here, except in *Sequoia* (8), their place being taken by resin cells. It would be natural to expect that the medullary rays also would be simpler, and this is indeed the case. The characteristically thick-walled, heavily pitted, parenchymatous ray cells of the Abietineae are replaced by thin-walled, sparingly pitted cells, and the ray tracheids characteristic of the Abietineae are lacking except under certain conditions to be described below.

The genus *Sequoia* undoubtedly stands nearest the Abietineae, since both living species have traumatic resin canals, and one fossil species (9), *S. Penhallowii*, has abundant pitting on the tangential walls of the ray cells, and crystals in the marginal cells like those of some species of *Abies*. Accordingly here if anywhere ray tracheids ought to be present, and GOTHAN has described them as of sporadic occurrence in the old wood of *S. gigantea* (10).

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Fig. 1 represents a radial section of the wood of *S. gigantea;* fig. 2 a few cells of this ray at a greater magnification. Mixed with the typical parenchymatous ray cells, there are large square cells whose bordered pits on radial, tangential, and vertical walls prove them to be tracheids. This ray is unique, all others being composed of normal, horizontally elongated, parenchyma cells as shown in other parts of fig 1; and it is significant to note that the branch from which this section was cut had been badly wounded. This ray, however, occurred on the side of the branch opposite the wound, while the rays in the wound cap itself were perfectly normal. On examining other wounded specimens of *S. gigantea*, ray tracheids were found occasionally, always however in close proximity to the traumatic resin canals. All these other ray tracheids, moreover, were long and low, with bordered pits only on the horizontal wall next the parenchymatous ray cells.

Fig. 3 represents a ray from *S. sempervirens;* fig. 4 the same ray under a greater magnification. The ray tracheid here shown is like those commonly seen in *S. gigantea*, horizontally elongated, with bordered pits exclusively on the horizontal wall. Miss GORDON (11) has described ray tracheids in *S. sempervirens* and I have found them in every wounded piece examined, but not elsewhere. JEFFREY concluded from a study of resin canals that *S. gigantea* was more primitive than *S. sempervirens*, and the larger and more vigorous ray tracheids of the former corroborate his conclusion.

DEBARY has reported (5) ray tracheids in the monotypic genus *Sciadopitys*. My material consisted of a repeatedly wounded branch and possessed scattered ray tracheids of the type shown in fig. 5. Those described by DEBARY, however, were like those in hard pines, with "irregularly thickened ridges, projecting inward like teeth, on the upper and lower sides." The toothed cells I have seen were very rarely ray tracheids, but were rather of the nature of septate tracheids. Fig. 6 shows one of them.

Traumatic ray tracheids have been described by JEFFREY in *Cunninghamia sinensis* (12). It is interesting to note that he found them on the side of the branch opposite the wound, a condition like that mentioned above in *Sequoia gigantea*.

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Specimens of *Taxodium distichum*, wounded and normal, of *Cryptomeria japonica*, and *Arthrotaxis selaginoides* were examined, but in none were ray tracheids observed.

CUPRESSINEAE

Of the genus *Chamaecyparis*, PENHALLOW (6) has described ray tracheids in *C. nootkatensis*, and absent elsewhere. In this species they are quite common, usually constituting the entire ray when one or two cells high, continuing for a time as such, and then becoming transformed into a parenchymatous ray. Careful examination, however, has revealed them in a number of other species. In *C. Lawsoniana* they are quite rare, but unquestionable. Fig. 7 shows their characteristic shape, long and low, with very small bordered pits next the parenchyma cells, two such pits being shown in the figure. *C. thyoides* and *C. plumosa* both show after injury tracheids of the same general appearance as those of *C. Lawsoniana*. A number of specimens of *C. pisifera* were examined before any ray tracheids were found. In one badly injured branch, however, there was a marked reversion to the thick-walled type of ray cell characteristic of the Abietineae, and between rows of these cells was a row of squarish tracheidal ray cells. In *C. obtusa* they seem entirely absent, even after injury.

In the closely allied genus *Cupressus* ray tracheids are much more common. Out of 7 species examined, they were present in 5; while of the other 2 species, only a small amount of material was available for study. The most frequent mode of occurrence is as an entire ray one to three cells high, though they have often been observed on the margin of higher rays. In this genus the relation to wounding is often diagrammatic. *C. guadalupensis*, after wounding, showed large numbers of ray tracheids. Fig. 8 shows a characteristic ray, but more commonly they constitute a ray one cell high, which soon turns into parenchyma; rarely they are marginal. *C. Macnabiana* presents the clearest case of traumatic reaction. Here frequently numbers of tracheidal rays one cell high start out immediately after a wound callus, extend through one or two years' growth, and then either die out or become transformed into parenchyma. *C. goveniana* showed the same

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thing, but to a less marked extent. *C. macrocarpa* was less favorable, but in one slightly wounded branch a few ray tracheids were observed. In *C. Benthami* they are very rare, but the material examined consisted only of a seedling with no wounds. Similarly a seedling of *C. tortulosa* failed to show any, and in *C. occidentalis* they seem to be entirely absent.

The southern hemisphere genus *Callitris*, with its sub-genus *Tetraclinus*, has been described by BAKER (13) as entirely without ray tracheids. JEFFREY, however, observed them in *Callitris* in connection with the leaf trace, and I have seen them quite widely distributed, but always in small numbers. Throughout the genus they are invariably marginal, never standing alone. Fig. 9 represents a characteristic ray tracheid in *C. arborea*. Two lots of material of this species were examined, and the mature wood of both contained ray tracheids of this type. There seemed to be no relation to injury, for they were equally abundant inside and outside a wound callus. Small branches, however, in neither lot showed ray tracheids. Fig. 10 demonstrates the type of tracheid characteristic of *C. calcarata*. Here they are longer and lower than in the above mentioned species, and, as there, the bordered pits are confined to the horizontal wall next the parenchyma cells. This material was entirely unwounded as far as could be seen. *C. columellaris* showed the same type of ray tracheids, even in normal tissue. *C. robusta* showed the largest number of tracheids of any species examined. They were present quite frequently in the mature wood, whether injured or not, but seem to be quite absent in the seedling stem. The ray tracheids are characteristically long and low, like those of *C. arborea*. *C. cupressoides*, as far as could be seen, lacks ray tracheids entirely, even in root wood. Fig. 11 shows a marginal tracheid in *Tetraclinus articulata*. They are present fairly abundantly in the mature wood, but are in general lacking in branches and twigs. One branch in which they were normally missing contained a few in the wound cap over a slight injury.

MAYR (14) has described ray tracheids in *Thuja plicata*, and I have found them quite common in both that species and in *T.*

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occidentalis. Figs. 12 and 13 show a characteristic region of *T. occidentalis*. The tracheids are invariably marginal, with small bordered pits communicating with the parenchymatous ray cells, and slightly larger ones on their slanting end walls. *T. globosa* and *T. orientalis*, as far as examined, are entirely without ray tracheids, while in *T. dolobrata* they are rare.

PENHALLOW (6) has described ray tracheids in *Juniperus nana*, but states that they are lacking elsewhere in this genus. Wounds, however, in almost every species examined, sufficed to recall them. In *Juniperus* they occur usually as large, very irregularly shaped cells, thickly pitted on the tangential wall, constituting the whole of a ray one cell high. Rarely, also, they occur on the margin of parenchymatous rays, in which case the horizontal wall only is pitted. Fig. 14 shows a ray from *J. californica*. Ray tracheids have been observed in the following species: *J. californica*, *J. virginiana*, *J. pachyploea*, *J. scopulorum*, *J. occidentalis*, *J. chinensis*, *J. chinensis* var. *alba*, *J. sabina*, and *J. barbadensis*. In *J. communis* they were missing altogether from wounded seedling, stem, and root, except in the wound cap of one stem which had been repeatedly injured near the ground. Three species failed to show any: *J. bermudiana*, *J. californica* var. *utahensis*, and *J. macrocarpa*.

The genus *Libocedrus*, according to PENHALLOW, lacks ray tracheids. Figs. 15 and 16, however, show a ray of *Libocedrus decurrens* with a marginal tracheid. Toward the left of fig. 15 there is a bordered pit; fig. 16 shows it in greater magnification. This section was cut from wounded material, but other wounds examined failed to recall ray tracheids. Traumatic wood of *L. chilensis* and *L. doneana* seemed to be without them also.

Actinostrobus and *Fitzroya* (*F. Archeri* and *F. patagonica*) both lack ray tracheids, as far as investigated.

PODOCARPINEAE, TAXINEAE, AND ARAUCARINEAE

Saxegothaea, *Dacrydium*, *Podocarpus*, *Phyllocladus*, *Taxus*, *Torreya*, *Cephalotaxus*, *Araucaria*, and *Agathis* were examined, but no ray tracheids were observed.

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Conclusions

To sum up, ray tracheids are present in *Pityoxyla* above the Middle Cretaceous; in all other fossil conifers they are absent. In living forms they occur normally in the Abietineae, traumatically in the Taxodineae and Cupressineae, but are invariably lacking in the Podocarpineae, Taxineae, and Araucarineae. Unless we are to assume that ray tracheids have developed independently in these groups, it is evident that the Taxodineae and Cupressineae must be related to the Abietineae. PENHALLOW admitted the relationship, but considered the cupressoid conifers ancestral to the Abietineae. The principle that traumatic tissue reverts to an ancestral type appears to be too strongly established to need discussion here. Applying this principle to the case in point, it must be seen that PENHALLOW has read the series in the wrong direction, and that the Taxodineae and Cupressineae are descended from rather than ancestral to the Abietineae. This conclusion might be questioned on the score that normally primitive regions, as first annual ring of seedling, root, cone axis, etc., fail to support the wound evidence by possessing ray tracheids. The answer to that appears to be simple: even *Pinus*, in which ray tracheids culminate, does not usually have them next the pith or in the cone axis. In other words, ray tracheids never made their way into the cone axis or first annual ring of any of the Abietineae, Taxodineae, or Cupressineae, but were characteristic only of mature wood. Consequently, now that they have become reduced in the last two families, they can be recalled only to the regions they once occupied normally. This conclusion as to the relative antiquity of the three groups, based on the distribution of ray tracheids alone, is corroborated by the conclusion reached by JEFFREY (4 and 8) from a study of resin canals.

The history of the development of ray tracheids, then, would be somewhat as follows. Up to the Middle Cretaceous, all *Pityoxyla* had simple medullary rays composed entirely of parenchyma. In the Middle Cretaceous they acquired ray tracheids. Some time between then and the Tertiary, a family sprung from these *Pityoxyla* characterized by the possession of ray tracheids. This family is the immediate ancestor of the Taxodineae and Cupressineae, while

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the original *Pityoxylon* line has persisted to the present day as the Abietineae. In some of them ray tracheids have become more and more elaborated (hard pines); in others they have become reduced until they occur only traumautically (*Abies*) or are entirely lacking (*Pseudolarix*). In the Taxodineae and Cupressineae they have become more and more reduced until they are present normally in only a very few species, and traumatically in certain others.

Since the taxads, podocarps, and araucarians never have ray tracheids, it is evident that if they came off from the Abietineae, it must have been at some time before the Middle Cretaceous, probably in the early Mesozoic.

To this suggested Upper Cretaceous origin of the Taxodineae and Cupressineae, it might be objected that in the Lower Cretaceous and Jurassic there are present *Cupressinoxyla*, together with leafy twigs, cone scales, cones, etc., which have been referred to *Sequoia* and allied forms. There is however nothing to prove that these woods belong to the Taxodineae or Cupressineae rather than to the podocarps or taxads, which, as pointed out above, probably originated very early in the Mesozoic. As to the twigs, cones, etc., wherever it has been possible to investigate their anatomy, they have been shown to be araucarians and not *Sequoia* at all (15 and 16).

Summary

1. Ray tracheids are present normally in *Pityoxyla* from the Middle Cretaceous on, and in the Abietineae.

2. Ray tracheids are present traumatically in the Taxodineae and the Cupressineae.

3. On the evidence of traumatic recapitulation of ancestral characteristics, it is evident that the Taxodineae and Cupressineae are descended from the Abietineae, having sprung from that line at some time after the Middle Cretaceous.

4. Since ray tracheids are universally absent in the Podocarpineae, Taxineae, and Araucarineae, these lines must have come off from the Abietineae at some time before the Middle Cretaceous.

5. These conclusions are corroborated by a study of geological records and of other anatomical structures, as resin canals, wood parenchyma, etc.

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I wish to express to Dr. E. C. JEFFREY my thanks for material and for advice throughout the course of this investigation, and to Mr. W. P. THOMPSON, Mr. A. J. EAMES, and Mr. E. W. SINNOTT for material.

CAMBRIDGE, MASS.

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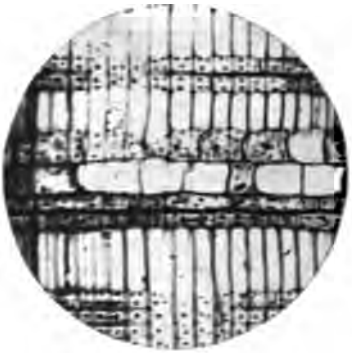

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EXPLANATION OF PLATES I AND II

FIG. 1.—*Sequoia gigantea;* ×250.
FIG. 2.—Same; ×500.
FIG. 3.—*Sequoia sempervirens;* ×200.
FIG. 4.—Same; ×600.
FIG. 5.—*Sciadopitys;* ×400.
FIG. 6.—Same; ×600.
FIG. 7.—*Chamaecyparis Lawsoniana;* ×700.
FIG. 8.—*Cupressus guadalupensis;* ×600.
FIG. 9.—*Callitris arborea;* ×600.
FIG. 10.—*Callitris calcarata;* ×600.
FIG. 11.—*Tetraclinus articulata;* ×600.
FIG. 12.—*Thuja occidentalis;* ×200.
FIG. 13.—Same; ×700.
FIG. 14.—*Juniperus californica;* ×600.
FIG. 15.—*Libocedrus decurrens;* ×200.
FIG. 16.—Same; ×700.

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THE LIFE HISTORY OF GLOEOTAENIUM

EDGAR N. TRANSEAU

(WITH PLATE III)

This peculiar alga was first collected by LOITLESBERGER at Ischl, Austria. On the basis of that material, HANSGIRG in 1890 described the genus and only known species, naming it for the collector, *Gloeotaenium Loitlesbergerianum* (1). He characterized the 2 and 4-celled families, with their encircling black bands. The chromatophore was stated to be star-shaped with a large central pyrenoid, and reproduction was limited to the multiplication by separation into two families. He thought the alga to be related to the desmids, and placed it together with *Spirotaenia* in a new family, the Pseudodesmidiaceae, which he conceived to be intermediate between the Desmidiaceae and the Palmellaceae.

In 1891 STOCKMAYER published a more detailed account (2) of the structure and life history, also based on a part of the material collected by LOITLESBERGER. He figures the 2 and 4-celled families and what he took to be a 1-celled individual. His 1-celled form, however, was either a diseased specimen or some other alga. The black band is described as originating by the gelatinization of the next to the outer layer of the mother cell wall in the plane of division. As gelatinization proceeds, the band is pushed inward until it occupies a position between the daughter cells. This process is preceded by the cell division and takes place about the same time that the outer gelatinous wall of the mother cell disappears. Gelatinous "caps" then develop near the poles of the mother cell, and as the second division takes place, these caps elongate in the plane of the second division until they fuse with the black band already formed. Inasmuch as polar "caps" also appeared in the 4-celled families, the author suggested the possibility of 8-celled families.

STOCKMAYER made it evident that the plant is not at all related to the Desmidiaceae, and that the black bands are hardly of sufficient importance to warrant the making of a new family. He con-

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cluded that it is most nearly related to *Oocystis* and *Nephrocytium* among the Protococcoideae.

WILLE (3) in 1892 included *Gloeotaenium* among the doubtful genera of the desmids in the *Natürlichen Pflanzenfamilien*.

TURNER (4) published WALLICH'S notes and figures of the plant from Eastern India in 1892. WEST has expressed some doubt as to the validity of this determination. I do not believe, however, that there can be the slightest doubt about the first four of his figures representing the 2-celled form. The other figures are questionable.

GUTWINSKI (5) figured the plant under the name of *Gloeocystis cincta* in his flora of Tarnopol, Austria.

DE TONI (6) corrected this name in 1895 and listed the localities in Austria, Italy, and East India in which *Gloeotaenium* had been found.

SCHMIDLE (7) reported the plant from Australia in 1896, and WEST (8) figured it in 1904 from the Island of Trinidad. In *The green algae of North America* COLLINS (9) reprinted one of STOCKMAYER'S figures and placed the genus near *Gloeocystis* among the Chaetophoraceae. Its occurrence, at Charleston, Ill., was reported by the writer (10) in 1911. In the recently issued supplement to the *Natürlichen Pflanzenfamilien*, WILLE places the genus next to *Pleurococcus* among the Pleurococcaceae.[1]

Gloeotaenium has been collected at three stations near Charleston, Ill.: the second pond west of the tile factory; Hodgen's pond; and the first pond west of the Big Four Railroad bridge across the Embarras River. All of these ponds are artificial. The first and second are a mile apart, and the third is about four miles east of the other two. Up to the present time the alga has been found only in collections from very definite areas in each of the ponds. In the tile factory pond it is the northeast corner, in Hodgen's pond the northwest corner, and in the Big Four pond the middle of the east side.

In the four years during which collections have been made from these habitats, no specimens have been recognized earlier than the

[1] Since this paper was written, *Gloeotaenium* has been reported by A. B. KLUGH from Colpitts Bay, Ontario (COLLINS, F. S., The green algae of North America, supplementary paper. Tufts Coll. Studies 3: 95. 1912).

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last week in June nor later than the last week in October. Its vegetative period, therefore, is about four months in this locality. Early in the summer of 1911 I started some cultures in small aquaria in the laboratory. These have now been under observation for seven months and have provided a valuable check on the field observations.

As shown in the accompanying figures, the mature plant occurs as 1-celled individuals, and as 2, 4, and 8-celled families. The 1-celled mature individual (fig. 5) is comparatively rare; it is spherical in form and may or may not retain parts of the outer gelatinous covering of the resting cell (figs. 1 and 3). The diameter of the outer wall averages 35 μ and of the cell 25 μ. The chromatophore is globose, parietal, comparatively thick, and may or may not contain a pyrenoid. In young cells the chromatophore is finely granular, in mature ones it is usually gorged with starch. The nucleus is centrally placed.

The 2-celled families are abundant and exhibit a great variety of forms. Some of these variations are shown in the figures. The mother cell wall may be nearly smooth and lenticular in form, or may be partially covered with a gelatinous secretion, or rarely may consist of two distinct layers, of which the inner one may be folded at the poles so that when viewed from the side it shows three ridges at either end (fig. 24). Except for the outermost wall, this last form closely resembles those from Australia. At the poles there are usually small "caps" formed of a tough gelatinous secretion. These appear to be secreted after the loss of the gelatinous covering of the resting stage. STOCKMAYER seems to have believed them to be on the inside of the mother wall, since he speaks of their fusion with the "bands" in the formation of the 4-celled families. I have not seen any specimens, however, in which this is the case.

The "caps" are regularly external to the mother wall and the "bands" are regularly internal. An appearance of an external band is sometimes made as in fig. 6, in which an equatorial ring of the gelatinous secretion, which surrounded the aplanospore wall during the rest period, remains.

The 2-celled families are 40–70 μ in length, 22–40 μ in breadth, and 20–30 μ in thickness. The cells are spherical, or depressed

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globose, sometimes flattened on the inner side, and sometimes on the outer. Between the two cells there is usually a gray, brown, or black band (figs. 8 and 9) composed of a more or less tough granular gelatinous secretion. This substance is at first colorless (fig. 4) and darkens with age. The color is partly due to total refraction and partly to a pigment. When the band is absent the caps also are wanting (fig. 10), but the band may be present without the caps. The mother cell wall is retained until late maturity, that is, until a short time (probably one or two weeks) before the breaking up of the family. In some cases this implies an existence during three or four months, and for those most favorably situated for development about a month.

My earliest outdoor record for the late maturity and aplanospore stage (figs. 17 and 18) is July 21. The disappearance of the mother wall is probably coincident with a rather rapid increase in the diameter of the vegetative cells from an average of 20 μ to an average of 30 μ. The cells remain attached to the band for a short period, but finally break away from this by their continued enlargement also. This last separation is clearly not due to the gelatinization of either cell wall or the band as stated by most authors. This is shown by the fact that after separation the band usually exhibits a ragged transparent edge, or occasionally there remains attached to it a thin wall from which the cell has escaped by tearing along the line of juncture with the bands. At the time of separation the cells may be thick or thin-walled, and may have divided internally (fig. 18). The thin-walled aplanospores germinate very soon by enlarging and dividing. The thick-walled aplanospores secrete a further gelatinous covering (fig. 1) and go through a rest period. Those cells which have already divided before separation may continue development (in the summer) or become thick-walled, secrete a gelatinous covering, and go into a rest period (in late autumn).

The 4-celled families are of two distinct types: (1) those having the cells in the same plane; (2) those in which the cells have a tetrahedral arrangement. In both the vegetative cells are similar to those of the 2-celled families. The 4-celled families with the cells in one plane (figs. 12 and 13) are about as abundant as the

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2-celled families in this locality. They vary in form from circular-lenticular (fig. 15) to elliptical-lenticular (fig. 11); from those having plane walls (fig. 14) to those having marked polar flattenings with a central ridge (fig. 16); from those with thick bands and caps to those entirely lacking the gelatinous secretion. When seen from the flat side, the bands when present are cruciform. They lie well within the mother wall, but may extend some distance beyond the cells (fig. 12). In the late maturity stage the mother wall is lost and the cells enlarge until they rather than the bands become the conspicuous feature (fig. 19). The cells may then separate at once or divide internally before separation (fig. 23). After separation of the aplanospores development or rest period follows as described under the 2-celled families. The tetrahedral 4-celled family (fig. 20) differs in having a close-fitting mother wall, in the necessarily different arrangement of the bands, and in the absence of polar caps. The life history is probably the same as for the preceding forms.

The 8-celled families are exceedingly rare. Out of the hundreds of specimens of the plant which I have examined from the collections and cultures, not more than a score of this type have been found. Of these there have been two forms about equally abundant: (1) those having the 8 cells arranged in the form of a cube with an edge 35–50 μ long, and (2) those with the 8 cells grouped more or less irregularly. These latter have in one or two instances resembled a cube that has been compressed so that the upper and lower faces are the shape of a rhombus.

These 8-celled families have a close-fitting mother cell wall until late maturity, when they are held only by the gelatinous bands. STOCKMAYER predicted the possibility of 8-celled families on the basis of the caps in the 4-celled forms, but he evidently had in mind families with 8 cells in the same plane.

The most important result of the cultures, however, has been to show that the mature colonies do not divide, that is, the 2-celled mature colonies do not form 4-celled colonies directly. When the bands are once formed they are permanent structures. Whether the family shall be 1-celled, 2-celled, 4-celled, or 8-celled is determined by the number of divisions that take place within the aplano-

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spore. I have found a number of cases where the divisions have taken place before the cell left the family, and before the heavy gelatinous outer covering was secreted (figs. 18 and 23). But it is probable that in most instances this division takes place after the resting period (fig. 2), for most of the aplanospores which I have examined showed no division and 1-celled mature individuals are comparatively rare.

That the propagative cells from 2-celled families do not necessarily form 2-celled families is shown in fig. 18, in which one of the cells has divided twice, the other but once. The development of the bands may be clearly understood from fig. 4. After germination (fig. 3) begins, the cells assume a more and more spherical form. Accompanying this process is the gradual separation of the cells and the secretion of the gelatinous layer from the adjacent cell walls.

My experience with *Gloeotaenium* both in the field and in cultures is thus far against the probability of zoospore production. The extreme localization of the collecting places in the ponds; the fact that it is most abundant on the bottom, and is brought to the surface only through the rising of other algae; and the fact that in the laboratory aquaria it is found only on the bottom, all point to the absence of swimming spores during the period I have had the plant under observation.

In the light of the above observations I should put the plant among the Scenedesmaceae near the genus *Oocystis*. The present description of the genus will require modification as follows:

Cells globose or variously flattened, solitary or united in families of 2, 4, or 8 cells, with wide and distinctly lamellate cell walls; the mother cell wall is frequently ornamented with folds and gelatinous disks opposite the cells; a dark-colored gelatinous layer usually extends between the cells of a family; chromatophore globose, with or without a pyrenoid. Reproduction by aplanospores and daughter cells.

The writer is under obligations to Mr. Frank S. Collins and Professor William Trelease for the loan of literature.

Charleston, Ill.

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EXPLANATION OF PLATE III

FIG. 1.—Aplanospore showing gelatinous secretion outside the cellulose wall; from culture; this and succeeding figures are from camera drawings.

FIG. 2.—Embryonic family about to enter resting period; from Hodgen's pond October 28, 1911; cell wall in optical section showing lamellae.

FIG. 3.—Germinating aplanospore; from culture.

FIG. 4.—Embryonic family showing early stage in the process of "band" formation; from Big Four pond July 10, 1911.

FIG. 5.—Mature one-celled individual; from Big Four pond July 10, 1911.

FIG. 6.—Two-celled family with equatorial remnant of gelatinous spore wall; from Hodgen's pond July 21, 1911.

FIG. 7.—Two-celled family showing band and caps; from Big Four pond July 10, 1911.

FIGS. 8 and 9.—Two-celled family, side and edge views, showing polar modification of the mother cell wall; from Big Four pond July 10, 1911.

FIG. 10.—Two-celled family lacking the gelatinous secretions; from Big Four pond July 10, 1911.

FIG. 11.—Four-celled family showing relation of bands and caps; from culture October 31, 1911.

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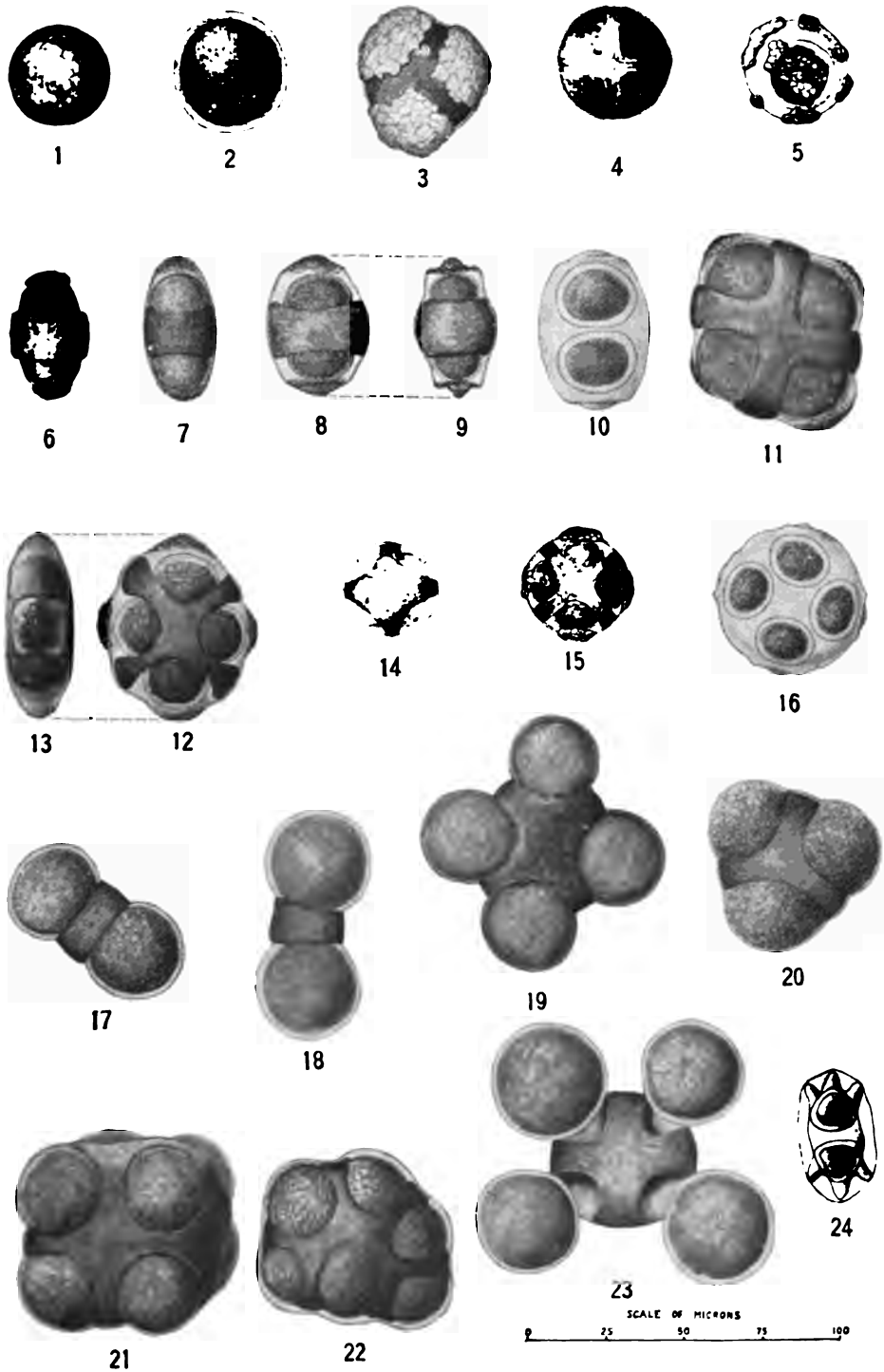

TRANSEAU on GLOEOTAENIUM

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FIGS. 12 and 13.—Four-celled family, side and edge views; from Hodgen's pond September 20, 1911.

FIGS. 14 and 15.—Young four-celled families; from culture July 25, 1911.

FIG. 16.—Four-celled family without gelatinous secretions.

FIG. 17.—Mature two-celled family; from culture October 10, 1911.

FIG. 18.—Contents of aplanospores dividing before separation.

FIG. 19.—Mature four-celled family; from Hodgen's pond July 21, 1911.

FIG. 20.—Tetrahedral four-celled family; from Hodgen's pond July 21, 1911.

FIG. 21.—Cubical eight-celled family; from Big Four pond July 10, 1911.

FIG. 22.—Irregular eight-celled family; from culture October 28, 1911.

FIG. 23.—Cells of four-celled family in which division has preceded separation; from culture October 28, 1911.

FIG. 24.—Double-walled two-celled family; from Big Four pond July 10, 1911.

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HYDRODICTYON AFRICANUM, A NEW SPECIES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 166

SHIGÉO YAMANOUCHI

(WITH SIX FIGURES)

The genus *Hydrodictyon*, as found in Europe, North America, and Asia, has been represented by a single species, *H. reticulatum* (L.) Lagerh. (*H. utriculatum* Roth.). Its normal life history, external appearance, habitat, and size at maturity are quite familiar to students of algae. Although little is known of the cytology of the zoospores and gametes, and the germination of the resting spores and polyeders, the general organization, with some details of the vegetative nuclear divisions and methods of forming spores and starch, have been described by VAUCHER, BRAUN, PRINGSHEIM, ARTARI, KLEBS, TIMBERLAKE, and HARPER.

In April 1912, shortly after Professor CHAMBERLAIN'S return from an extensive trip through Australia and South Africa, some soil was sent to him by Miss EDITH STEPHENS of the South African College. The soil was secured on the Valkenberg Vlei, near Cape Town, and was supposed to contain spores of the liverwort *Riella*. Some individuals of *Riella* appeared in the culture, but in addition to these there appeared a new species of *Hydrodictyon*, which we shall call *H. africanum*. The following description is based upon the material from this culture.

Early in May there appeared on the bottom of the tank, just above the surface of the soil, a number of green spherical bodies of barely recognizable size, which had the general aspect of *Botrydium*. As growth progressed, the spherical bodies, instead of being groups of solitary cells, were seen to be connected into nets. The nets are made up of 60 or more globular cells which form irregular meshes, arranged in hexagons, heptagons, or octagons, or sometimes simply in broken chains. The nets grow rapidly. Each cell does not grow into an ellipsoidal cylinder as in *H. reticulatum*, but remains spherical or oblong. The cells have remarkable

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turgidity, so that when the net is supported at one end, the entire plant is kept straight and can be held up in any position without bending or drooping. When the plants grow larger, the turgidity of the cells remains the same, but the connection between cells is by only a small portion of the surface and consequently it is impossible to move the plant without breaking the cells apart. As the plant grows, the connection becomes less and less secure, so

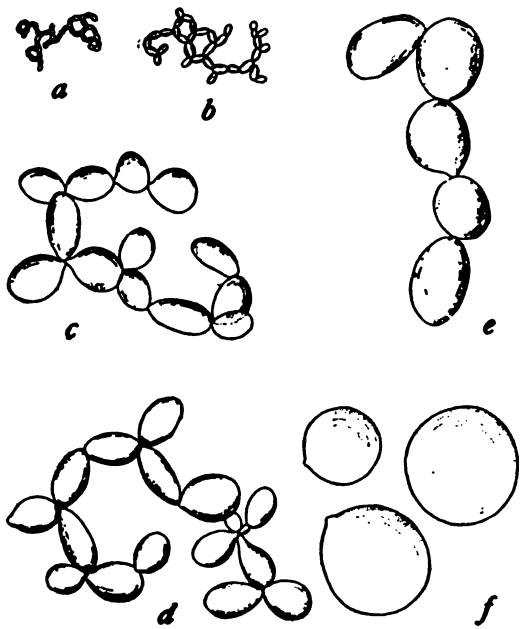

FIG. 1.—*Hydrodictyon africanum*, showing successive stages of development: *a*, May 2, 1912; *b*, May 12; *c*, May 20; *d*, June 12; *e*, June 20; *f*, October 12.—Sketches from living material, natural size.

that the cells fall apart at the slightest touch or even by a movement of water caused by small crustaceans, until finally the nets are broken apart into solitary cells, or coenobia. During this development, the coenobium has reached an enormous size, the diameter often being more than 1.5 cm. Sketches from living material in successive stages from late April to the middle of June are shown in fig. 1.

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The dissociated cells remained up to the end of June, and then apparently began to disorganize. Finally they disappeared, and either the entire stock has died or has sunk to the bottom and become buried in the soil in the resting spore or polyeder stage. That the plants should have broken up into solitary cells and that they should have reached such an enormous size might have been thought to be due to the change of environmental conditions, like change in habitat, the gradual change in the density of the water in the tank, or changes in temperature and food. However, another supply of the material, collected in October in the original locality by Miss STEPHENS, showed that the form behaves similarly in nature. This material consists of the various stages as they appeared in the culture, from the young nets of small cells, through broken chains made up of a smaller number of larger cells, to the solitary coenobia. Fig. 1, *f*, shows the last stage, in which the coenobium is slightly larger than those obtained in our own cultures.

It is now clear that the form in nature passes through the same course of development as in our cultures in the laboratory, that is, there is first a net, the cells of which break apart by their own peculiar turgidity and looseness of connection, until finally, the cells which were the sides of the meshes of the net become solitary and live for several months as independent forms. This habit shows most clearly the colonial organization of *Hydrodictyon*.

The soil before starting the culture in the laboratory was not examined for the possible presence of *Hydrodictyon*, but there could be no reason to suspect the previous existence of the plant in the net form in the dried condition, and therefore it must have been in the resting spore condition, characteristic of green algae, or in the polyeder condition, if this form follows the life cycle of *H. reticulatum*, as described by PRINGSHEIM. In any event, we first recognized a rather irregular net coming out of the soil in the tank, which recalls, according to PRINGSHEIM, the product of the germination of a polyeder, though in his description the product consisted of 200–300 cells, while in *H. africanum* there are at most less than 70 cells. The formation of new nets inside the mother cell, which is familiar in *H. reticulatum*, was not observed in this form. The formation of gametes was not observed in the living condition, but

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was found in fixed material. Consequently, the final product of the coenobium may be gametes, which escape from the cell and after fusion form resting spores. These directly or with the interpolation of a polyeder stage may repeat the cycle.

Not only does this form differ from *H. reticulatum* in size and habit, but there are points of fundamental difference in the structure of the cell, the most remarkable of which are the presence of numerous definite plastids and the formation of starch, not by the fragmentation from the pyrenoid, but in the plastids. These characters which differ from *H. reticulatum* seem to us to be a sufficient basis for a new species, which may very properly be called *Hydrodictyon africanum*.

The general cell structure, nuclear division, and starch formation deserve a brief account. The protoplast of the coenobium is surrounded by a thick wall and occurs as a thin parietal layer, a large vacuole occupying the center. The cell wall consists of three different layers. The protoplasm may be conveniently described as consisting of three parts: *Hautschicht*, the outermost part, directly in contact with the cell wall; plasma membrane, the innermost part which lines the central vacuole; and between these two the main cytoplasmic body, which contains numerous nuclei, plastids, pyrenoids, starch grains, and small vacuoles (fig. 2).

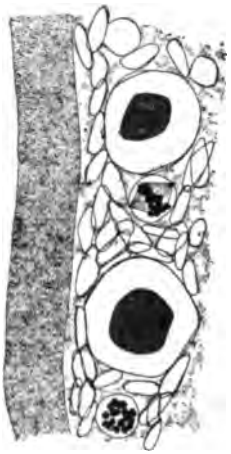

FIG. 2.—Part of a section of a single coenobium: fixed May 20, 1912.—×1500.

The nucleus varies greatly in size at different stages of the division (fig. 3). In the resting stage it is very small, about as large as the shorter diameter of the plastid. It then gradually increases in size. There is a scanty chromatin network and a single nucleolus. When the nucleus has reached its full size, the nuclear network becomes impregnated with a large amount of chromatin. Knots appear in the network and eventually develop into 18 chromosomes. The nuclear membrane is always present until just after metaphase. A centrosome is recognizable from prophase to late anaphase. After telophase, new daughter nuclei

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are formed, which grow and divide. No case of amitosis was observed. The mitoses in the cell do not take place simultaneously, so that every stage in the division is shown even in a single section of the cell.

The presence of definite chromatophores or plastids has been a matter of discussion among various workers on *H. reticulatum*, but in this new form numerous plastids lie in contact with one another in the middle part of the cytoplasm. The plastid in its earlier stages has an irregular platelike or spindle-like form, and it is denser in the outer region than in the center. A most interesting and important feature in the new form is that the plastids

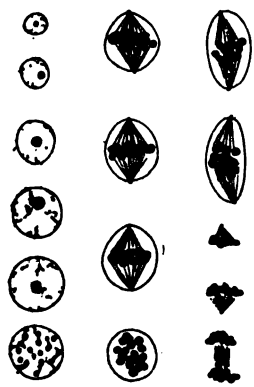

FIG. 3.—Mitotic figures of various stages.—×1500.

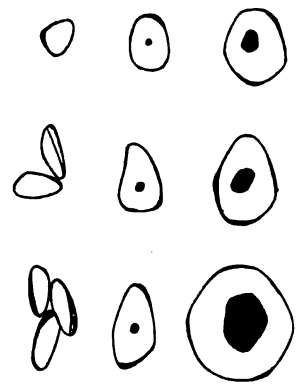

FIG. 4.—Stages showing the formation of pyrenoids from plastids.—×1500.

have two functions, one to produce characteristic pyrenoids and the other to form reserve starch grains.

The formation of pyrenoids from the plastids is as follows. The plastid at first is more dense in the outer part than in the center; and then it increases in size. A deeply staining portion differentiated from the plastid first appears in the center of the body as a small dot, during the growth of the plastid. As the general outline of the plastid grows, the dot also grows, and finally the body of the plastid reaches its full size and assumes a somewhat spherical or slightly angular form; the dot inside also enlarges and assumes a spherical or slightly angular shape. Thus there is established the

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so-called pyrenoid, spherical in form and consisting of a denser central portion surrounded by the body of the plastid (fig. 4).

The formation of starch grains by the direct fragmentation of the pyrenoid as described by TIMBERLAKE does not occur in this new form. The method of starch formation is as follows. In a part of the body of the plastid near its margin a starch grain is formed either by secretion, as MEYER believes, or in some other way. The starch grain grows and finally reaches a size equal to that of the pyrenoid. The starch thus formed is more abundant toward the plasma membrane (fig. 5).

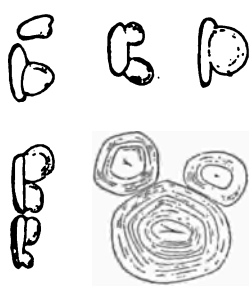

FIG. 5.—Stages showing the formation of starch grains by plastids.—×1500.

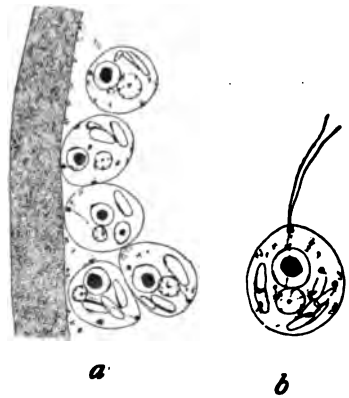

FIG. 6.—Gametes: *a*, part of a section showing the gametes lying near the cell wall, ×1200; *b*, a single gamete, ×1500.

The gamete formation was not observed in living cells, but in fixed material many cases of cells were observed in which a majority of the spores had escaped, still leaving a number of spores within. Whether the spores are zoospores or gametes was not ascertained, but judging from the condition in *H. reticulatum* they should be gametes.

Hydrodictyon africanum Yamonouchi, sp. nov.—Young net of about 60 coenobia; when old, coenobia becoming solitary by breaking apart on account of their great turgidity and loose connections; coenobia deep green, but yellow with age, spherical or oblong, and finally attaining an enormous size, as large as 1.5 cm.; the coenobia live a long time in the solitary condition.

TYPE LOCALITY.—Valkenberg Vlei, near Cape Town, South Africa.

UNIVERSITY OF CHICAGO

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REVEGETATION OF A DENUDED AREA

H. S. CONARD

(WITH TWO FIGURES)

One-half mile west of Cold Spring Harbor station on the Long Island Railroad, extensive changes in the roadbed are in progress. In straightening, widening, and changing the grade of the road, the hillside has been cut away, and the materials so obtained have been dumped directly downhill from the cut to make a wide level shelf for the tracks. Where the new level crosses the old grade of the hillside, the soil was practically undisturbed and a curved line of vegetation has grown up from the old roots. On the side of this line toward the hill the earth is newly exposed. It has been buried since the glaciers left it. On the other side of the line, the ground consists of the material dug away from the adjacent hill by steam shovels and dumped at once or after a short haul in cars. The digging was done in March and April 1911. The material moved is coarse sand and fine gravel of the morainic hills of the north side of Long Island. The hillside faces south, and was clothed with a vegetation typical of such a dry, sunny situation in this region.

On the apparently denuded area, the prospective roadbed, many plants are already (July 1911) well developed. A study of the nature and origin of these has proven of interest and is here presented. Sixty species of angiosperms and one fern make up the present flora of the newly made shelf; 53 of these are now to be found growing on the hillside above the cut. Of the plants found both above and below, 39 are long-lived perennials. All of these except *Smilacina racemosa*[1] and *Desmodium canescens* were growing in the made ground from pieces of root, rhizome, or "crown" of old plants carried down from the hillside in the digging. The fragments had been tumbled in promiscuously with the earth, and those near enough the surface had sprouted. Thus we have a large experiment in the roughest kind of transplanting of 37 species

[1] The nomenclature of the new GRAY'S *Manual* has been followed.

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during their resting period. The *Smilacina* and *Desmodium* mentioned above grew in the band of vegetation where the old hillside grade intersects the new level. They had not been transplanted, but were covered with about three inches of fresh sand.

Whether the transplants were roots or rhizomes is of but slight importance. So far as we could determine by surface inspection, root propagation is shown by the following:

Myrica Gale, M. asplenifolia (root 6 in. by ½ in.), Sassafras variifolium (6 in. by ¼ in.), Rubus villosus (3 in. by ⅛ in.), Robinia Pseudo-Acacia (4–6 in. by ⅛ in.), Lespedeza fruticosa (?), L. repens, Euphorbia Ipecacuanhae, Rhus glabra (6–8 in. by ½ in.), R. copallina (6 in. by $\frac{3}{16}$ in.), Vaccinium pennsylvanicum (4 in. by ⅛ in.), Asclepias amplexicaulis (3 in. by ½ in.).

Pieces of rhizome give rise to new plants in the following:

Pteris aquilina, Smilax glauca, S. rotundifolia, Aralia nudicaulis (14 in. by ½ in.), Lespedeza virginica (?).

The entire plant or the crown with more or less of root had been moved down bodily in the following:

Andropogon scoparius, Panicum sp., Cyperus filiculmis, Stenophyllus capillaris, Carya alba (stump), Quercus marylandica (stump), Q. alba (stump), Rumex acetosella, Prunus serotina (stump), Baptisia tinctoria, Desmodium nudiflorum, D. rotundifolium, Stylosanthes biflora, Oxalis corniculata, Helianthemum canadense, Viola pedata, Thaspium aureum (?), Plantago major, Eupatorium hyssopifolium, Solidago altissima, S. odora (?), S. tenuifolia, Aster (2 spp. not identified), A. linariifolius, Sericocarpus asteroides, Achillea millefolium, Taraxacum officinale.

Seedlings of the following plants were found in the congenial sand of the new exposure, though no seedlings of *Myrica*, *Castanea*, *Baptisia*, or *Tephrosia* were seen on the hillside. The other species named, whose seedlings were found in both habitats, are nearly all annuals.

Myrica asplenifolia, Castanea dentata, Phytolocca decandra, Mollugo verticillata, Portulacca oleracea, Baptisia tinctoria, Tephrosia virginiana, Trichostema dichotoma, Linaria canadensis, and Ambrosia artemisiaefolia.

The following plants of the new ground were not found at all on the hillside:

Avena sativa, Polygonum hydropiper (?), P. convolvulus, Acalypha virginica, Oenothera biennis, Xanthium canadense (?).

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These are such common weeds everywhere that their appearance causes no surprise. Nevertheless it would be interesting to know how they came in. *Avena*, of course, and perhaps others were brought by horses.

Turning to the hillside, we find 25 species[2] which are not yet represented on the new ground below. A few of these deserve notice. For example, a part of the hill is literally covered with

FIG. 1.—A wide level shelf for the track

Gerardia pedicularia, both rosettes and flowering plants. Why did none of these survive transplanting? Perhaps their parasitic habits are partly responsible. If so, the plant must be an obligate parasite, even if only hemiparasitic. *Deschampsia flexuosa* is much more plentiful on the hillside than *Andropogon*, but none of it

[2] The plants found on the hillside but not below are Deschampsia flexuosa, Carex (2 spp.), Corylus americana, Quercus stellata, Amelanchier canadensis, Lupinus perennis, Linum virginianum, Acer rubrum, Psedera quinquefolia, Hypericum gentianoides, Lechea villosa, L. intermedia, Cornus sp., Chimaphila maculata, Gaylussacia baccata, Verbascum Thapsus, Gerardia pedicularia, G. flava, Chrysopsis mariana, Solidago bicolor, Antennaria neglecta, Erechtites hieracifolia, Hieracium venosum, and H. scabrum.

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appears below. The new exposure is very sunny, and therefore unfavorable to *Deschampsia*. Perhaps also its root system may not be disturbed without serious injury. Two species of *Lechea* and one of *Hieracium* (*H. venosum*) are the next most plentiful hillside plants which did not survive transplanting. We have no explanation for this. Large clumps of *Lupinus perennis* and *Tephrosia virginiana* occur at one part of the hill. It seems strange

FIG. 2.—On the apparently denuded area many plants are already well developed

that no transplanted specimens were found. The remaining species of the hill were not numerous enough to give any large chance of their finding a possibility of survival on the new ground.

The meaning of this record is in several respects very clear. (1) An area denuded in winter or early spring receives few if any disseminules by any agency save that of man and domestic animals. Plants are not traveling at that season. (2) An apparently denuded area may contain viable fragments of a rather large flora. (3) If the disturbance occurs during the resting season of vegetation, new plants will arise from many fragments which would perish at any other season. For the resting plant contains nourishment to enable

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it to start new growth, and most perennials put out a whole new system of absorptive roots as well as a whole new foliage each year. The extent of the new root system is greater than many people suppose. (4) As a corollary to this it follows that most plants can be successfully transplanted, even by very rough methods, during the resting period. This is why I can get three good grape vines by mail in a package but little bigger than a lead pencil, and all of them grow vigorously. It is, indeed, the basis of the whole nursery business. (5) Propagation from bits of resting roots and rhizomes is possible in many plants where this method is not usually practiced. But the practice has become much more common commercially in the last ten years, owing to the keen observation of the best gardeners. It must be stated that in many cases of the transplants noted in this account, the new rootage seemed more meager than the production of shoots. Whether all of the sixty-one species will survive, or, in the terminology of CLEMENTS, whether their rather violent migration will be followed by ecesis, remains to be seen.

COLD SPRING HARBOR, L.I.

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CURRENT LITERATURE

NOTES FOR STUDENTS

Metabolism of fungi.—The problem of the necessity of calcium for fungi has been attacked in different ways by HORI and by Mlle. ROBERT. HORI[1] relied on removing the calcium from his solutions by precipitating it by means of an oxalate. To a solution of "ame" (rice treated with malt extract) in bouillon, he added potassium sulphate and potassium oxalate. In the solution thus obtained *Aspergillus niger*, *A. flavus*, and *Penicillium glaucum* developed well, while *Cephalothecium roseum*, *Rhizopus nigricans*, *Rammularia Citri*, *Botrytis tenella*, *Sclerotinia Libertiana*, and a species of *Entomophthora* developed poorly or not at all. All the fungi developed well in the same solution to which potassium sulphate but no oxalate had been added. From the fact that a number of the fungi did not develop in a solution containing 0.5 per cent of potassium oxalate, the author concludes that these probably require calcium for their development. The conclusion is scarcely justified, since it is not at all probable that calcium is completely removed by potassium oxalate from solutions containing organic substances. The same criticism applies to the experiments of WEIR, which have already been reviewed in this journal.[2]

The problem has been attacked in a more critical manner by Mlle. ROBERT,[3] who worked with *Aspergillus niger*. She showed that the results of the earlier investigators (RAULIN, MOLISCH, LOEW), who came to the general conclusion that calcium was not necessary for the life of most fungi, were due to the fact that they relied on the so-called "pure salts" of commerce. Mlle. ROBERT finds that these "pure salts" always contain calcium. It is thus evident that the conclusion generally reached by those investigators, that calcium is not necessary for the life of fungi, was reached on insufficient grounds. Mlle. ROBERT purified the salts she used until no traces of calcium could be detected in them. In culture solutions made from such purified materials *Aspergillus niger* grows equally well whether calcium is added or not. From dilute solutions containing up to 2.5 mg. per 250 cc. of solution, the calcium is removed almost quantitatively by the fungus and can be recovered in the ash. From stronger solutions containing 10–100 mg. per 250 cc. about 80 per cent of the calcium is removed. When much calcium is absorbed, both the yield and

[1] HORI, S., Haben die höheren Pilze Kalk nötig? Flora **101**:447, 448. 1910.

[2] BOT. GAZ. **53**:88. 1912.

[3] ROBERT, MLLE., Influence du calcium sur le développement et la composition minérale de l'*Aspergillus niger*. Compt. Rend. **153**:1175–1177. 1911.

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the ash of the fungus are increased, but the increase corresponds to the amount of calcium absorbed. The increase of the ash corresponds to the amount of calcium absorbed calculated as calcium carbonate. It appears from this paper that calcium is of no importance for the development of *Aspergillus niger*, but that when present in the culture medium, it is absorbed and increases the yield and ash only by the amount absorbed.

In another paper[4] Mlle. ROBERT concludes that the calcium absorbed from solutions by *Aspergillus niger* is quantitatively fixed in the form of calcium oxalate. This conclusion is based on analyses of mycelia from a large number of cultures. Although it was necessary to determine the calcium and the oxalic acid in different cultures, the determinations showed that the oxalic acid present in the mycelium corresponded to the quantity calculated on the assumption that all the calcium fixed was present in the form of calcium oxalate. Owing to the fact that in the cultures without calcium the oxalic acid formed diffuses into the medium, mycelia from such cultures always contain less oxalic acid than those with calcium.

SAUTON,[5] studying the effect of iron on spore-formation of *Aspergillus niger* grown on RAULIN'S solution free from iron, finds that in the absence of iron no spores are formed by this fungus. This fact, while not mentioned specifically by RAULIN, seems nevertheless not to have escaped his notice completely, for he states that in the absence of iron spores become fewer and fewer in proportion to the number of crops of fungus grown on the same solution. When iron is added to cultures free from iron, the yield increases and spores are produced. Cultures with 0.1 mg. of iron per 100 cc. of liquid and those with 1.0 mg. per 100 cc. gave practically the same yield, but spore-formation was almost suppressed in the 0.1 mg. cultures, while those with 1.0 mg. per 100 cc. were black with spores. The cultures without iron made feeble growth and produced no spores. Since there was no difference in growth but a great difference in spore-production between cultures containing 0.1 mg. of iron per 100 cc. of liquid and those containing 1.0 mg. per 100 cc., the author concludes that iron has a specific influence on spore-formation. The possibility that toxic substances are produced in the absence of iron had already been suggested by RAULIN, who noted that in cultures without iron a substance is formed which he regarded as sulphocyanic acid, and FERNBACH had shown that in the presence of ammonium sulphocyanate *Aspergillus niger* grows naturally but does not form spores. SAUTON doubts the formation of sulphocyanic acid, since the liquid from cultures containing 0.1 mg. of iron per 100 cc. (in which spore-formation is almost inhibited) does not give the red color reaction with ferric salts. In cultures without iron, however, a faint red color reaction

[4] ROBERT, MLLE., Mode de fixation du calcium par l'*Aspergillus niger*. Compt. Rend. **154**: 1308–1310. 1912.

[5] SAUTON, B., Influence du fer sur la formation des spores de l'*Aspergillus niger*. Compt. Rend. **151**: 241–243. 1910.

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indicating colorometrically a concentration of 0.005 per cent of sulphocyanic acid could be obtained, but the equivalent of that concentration of ammonium sulphocyanate is without effect on the fungus. That other poisonous substances are formed is doubted by the author, because if to a solution free from iron, on which *Aspergillus* has grown for three days without forming spores, iron is added the culture becomes covered with spores in 24 hours. The suppression of spore-formation is therefore due to the lack of iron and not to a toxic substance. Furthermore, since ferric sulphocyanate also inhibits spore-formation, the favorable effect of iron cannot be due to a possible neutralization of sulphocyanic acid by iron. The author notes a similarity in the behavior of cultures without iron and those suffering from lack of oxygen, and suggests that iron is possibly instrumental in bringing about oxygen fixation.

RAULIN's observation, confirmed by SAUTON, of the occurrence in cultures of *Aspergillus* of a substance giving a red color reaction with ferric salts and therefore regarded as sulphocyanic acid, is of interest in view of the fact that GOSIO in Italy and ALSBERG and BLACK in this country find in cultures of other molds phenol-like substances giving red color reactions with ferric salts.

A later paper by SAUTON[6] consists essentially of a republication of the foregoing paper with some additional observations, although in the meantime the author working with JAVILLIER had published results (reviewed below) leading to an entirely different conclusion from that reached in these two papers. It appears from SAUTON's second paper that the need of iron is not general among fungi, for while *Aspergillus niger*, *A. fumigatus*, *Penicillium glaucum*, and *P. candidum* make only feeble growth on RAULIN's solution free from iron, *Mucor Mucedo*, *Rhizopus nigricans*, and *Racodium coellare* thrive well without iron, or at least with only such minute traces of it that it is impossible to detect them. Since the publication of SAUTON's first paper, BERTRAND and JAVILLIER have called attention to the effect of manganese on the growth of *Aspergillus niger*, without however giving attention to the influence of that element on spore-production. SAUTON finds that the substitution of manganese for iron also stimulates spore-production. He has not been able, however, to obtain sulphate of manganese, which he employed, entirely free from iron, and although the traces of iron thus added were extremely minute, he does not draw any conclusion as to the possibility of substituting one of these elements for the other. Further evidence that the inhibition of spore-production is not due to the formation of sulphocyanic acid was obtained from an experiment in which both sulphur and iron were absent. Although the formation of sulphocyanic acid was not possible under these conditions, spore-production was nevertheless inhibited. On the addition of sulphate of iron spores were formed, showing that it is not sulphocyanic acid which inhibits spore-formation.

[6] SAUTON, B., Influence du fer sur la culture de quelques moisissures. Ann. Inst. Pasteur 25:922–928. 1911.

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Conclusions very different from the foregoing regarding the special rôle of iron in spore-formation are reached by JAVILLIER and SAUTON[7] in the paper mentioned above. According to this paper iron does not possess a special rôle in the formation of spores, but in the absence of iron, spore-formation is inhibited by the zinc in RAULIN's solution. If both zinc and iron are excluded, spores are readily formed, just as they are when both of these elements are present. If zinc alone is present, spore-formation is inhibited.

The authors suppose that the zinc, which was observed by RAULIN to have a favorable effect in the culture solution proposed by him, exerts toxic effects when the mycelium is poorly nourished through the lack of iron or from some other cause. In the ash of mycelia grown on solutions without iron, no iron was found, although the reactions employed were capable of indicating the presence of 1/1000 of a milligram of the element; hence the authors conclude that if iron is at all essential for spore-formation, the quantity required is so small that it cannot be detected in the ash of the mycelium. It is also stated that the substance giving the red color with ferric salts and supposed by RAULIN to be sulphocyanic acid is not formed when both iron and zinc are absent.

A search for an explanation of the favorable effect, noted by RAULIN and others, of zinc on the growth of *Aspergillus* has led JAVILLIER[8] to investigate the action of that metal on the secretions of invertase by *Aspergillus niger*. The results are suggestive as showing the influence of certain substances on the diffusion of other substances through the protoplasmic membrane. He finds that in cultures free from zinc the liquid does not invert sugar, while culture solutions containing zinc invert sugar readily after *Aspergillus niger* has been grown on them. This difference, however, does not indicate that no invertase is formed in the absence of zinc, for sugar was consumed in both cultures. In cultures free from zinc the enzyme does not diffuse into the liquid.

Several notes have been published by BERTRAND and by BERTRAND and JAVILLIER on the influence of manganese on *Aspergillus niger* and on the relations of this element to zinc and iron when present in the culture medium. Manganese[9] in dilute solutions is found to have a favorable action on the growth of this mold. In solutions containing manganese in concentrations ranging from 1 part in 1,000,000 to 1 part in 100, there was a gradual increase

[7] JAVILLIER, M., et SAUTON, B., Le fer est-il indispensable à la formation des conidies de l'*Aspergillus niger?* Compt. Rend. **153**:1177–1180. 1911; also Compt. Rend. Soc. Biol. **71**:589, 590. 1911.

[8] JAVILLIER, M., Influence de la suppression du zinc du milieu de culture de l'*Aspergillus niger* sur la sécrétion de sucrase par cette Mucédinée. Compt. Rend. **154**:383–386. 1912.

[9] BERTRAND, G., et JAVILLIER, M., Influence du manganèse sur le développement de l'*Aspergillus niger*. Compt. Rend. **152**:225–228. 1911; also Bull. Sci. Pharmacologique **18**:65–73. 1911; also Bull. Soc. Chim. France. pp. 212–220. 1912.

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of yield with increasing concentration of the metal. An increasing quantity of the metal was found in the ash, although even in dilute solutions the element was not removed quantitatively, like calcium or zinc. A concentration of 1 part in 50 was deleterious.

Unexpected results[10] showing the sensitivity of plants to extraordinarily minute traces of substances were obtained with manganese in extreme dilutions. After every available means had been used for removing manganese from the ingredients of the culture solutions, it was found that the addition of 1 mg. of manganese in 1,000,000 liters produced a marked increase in yield, while in some cases even the effect of 1 mg. in 10,000,000 liters was noticeable. The effect of manganese in such extreme dilutions is attributed to action of a catalytic nature. The necessity of taking into consideration in physiological experiments the possibility of effects being produced by such minute traces of substances which may be present as impurities in the materials used is pointed out.

The simultaneous addition[11] of zinc and manganese in concentrations at which these metals individually increase the yield of fungus produces a greater yield than the addition of either metal alone. The favorable concentrations were: zinc, 1 part in 100,000 to 1 part in 25,000,000; and manganese, 1 part in 500 to 1 part in 25,000.

To determine if either of these two metals exerted an influence on the absorption of the other, the quantity of manganese absorbed in the presence of zinc was compared[12] with that absorbed from solutions without zinc. The results show that in general the percentage of manganese in the dry weight of the fungus is greater in the presence of zinc. The proportion varies somewhat according to the concentrations of manganese and zinc. The effect of the zinc is more marked in dilute solutions and disappears in more concentrated solutions.

To manganese is attributed a special rôle in spore-formation formerly ascribed by RAULIN and by SAUTON to iron. The effect noted by these investigators BERTRAND[13] believes to be due to the introduction of minute traces of manganese from which it is difficult to free some of the other salts used in RAULIN's solution. He finds that when *Aspergillus* is grown in a solution free from manganese, but containing both zinc and iron (1 part in 100,000) no

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[10] BERTRAND, G., Extraordinaire sensibilité de l'*Aspergillus niger* vis-à-vis du manganèse. Compt. Rend. **154**:616–618. 1912.

[11] BERTRAND, G., et JAVILLIER, M., Influence combinée du zinc et du manganèse sur le développement de l'*Aspergillus niger*. Compt. Rend. **152**:900–902. 1911; also Bull. Sci. Pharmacologique **18**:321–327. 1911.

[12] ———, Influence du zinc et du manganèse sur la composition minerale de l'*Aspergillus niger*. Compt. Rend. **152**:1337–1340. 1911.

[13] BERTRAND G., Sur le rôle capitol du manganèse dans la formation des conidies de l'*Aspergillus niger*. Compt. Rend. **154**:381–383. 1912.

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spores are produced. If a trace of manganese is added, the surface becomes black with conidia.

A later paper by BERTRAND and JAVILLIER[14] consists of recapitulation of the data in the foregoing papers by them, together with a general discussion of the results obtained.

The availability of various nitrogenous compounds as sources of nitrogen for fungi has been investigated by BRENNER, by RITTER, and by KOSSOWIC. BRENNER[15] in a brief paper gives the general results of an investigation designed to determine the relative value of various nitrogenous compounds for the nutrition of *Aspergillus niger*. The compounds were given in a concentration equivalent in nitrogen to a 0.5 per cent ammonium chloride solution. The nutritive value of the substances was determined by ascertaining the time required for the cultures to attain a maximum weight on a given substance. Both the time required for reaching a maximum development and the weight of fungous substance produced were taken into consideration. By analysis of the fungus crops and the residual culture medium, the qualitative and quantitative interchange of nitrogen between the fungus and the medium was determined. The results showed that a large number of compounds are not suitable sources of nitrogen. Of this category are free ammonia, sodium nitrite, ammonium valerianate, and potassium cyanide, all of which are poisonous, and tetramethylammonium chloride, nitroguanidin, nitromethane, isoamylacetate, pyridin chloride, and piperidine chloride, which are not assimilable. The order of nutrient value of the other compounds tried is somewhat as follows: first, ammonium lactate, ammonium tartrate, asparagin, ammonium succinate, and ammonium oxalate; second, the ammonium salts of sulphuric, hydrochloric, nitric, and phosphoric acids, and carbamid; third, ammonium acetate, ammonium formate, nitrosodimethylamin chloride, sodium nitrate, pyridin nitrate, normal and isobutylamin chloride, guanidin nitrate, and guanidin chloride. Of less nutritive value are isoamylamin chloride, hydroxylamin sulphate, benzylamin sulphate, dicyandiamid, and perhaps acetonitril.

A study of the composition of the fungus and the changes in the medium showed that after a period of growth of about 4 days, processes of degeneration began in parts of the fungus. These were accompanied by the secretion of nitrogen as ammonia or as organic nitrogenous compounds. As a rule, regardless of the nature of the compounds, about one-half of the nitrogen present in a solution containing the nitrogen equivalent of a 0.5 per cent ammonium chlorid solution was taken up by the first crop of fungus grown. Subsequent crops having less nitrogen at their disposal contained a lower percentage of

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[14] BERTRAND, G., et JAVILLIER, M., Action du manganèse sur le développement de l'*Aspergillus niger*. Ann. Inst. Past. **26**:241–249. 1912.

[15] BRENNER, W., Untersuchungen über die Stickstoffernährung des *Aspergillus niger* und deren Verwertung. Ber. Deutsch. Bot. Gesells. **29**:479–483. 1911.

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nitrogen than the first crops on the same solution. No general conclusions were deducible from a quantitative study of the residual culture fluid.

RITTER[16] in confirmation of results published in a former paper emphasizes the fact that *Aspergillus glaucus*, *Cladosporium herbarum*, and *Mucor racemosus*, known as "nitrate fungi" on account of their supposed preference for nitrogen from the nitrate ion, thrive equally well or better on ammonium salts. The slight alkalinity arising in cultures with potassium nitrate is, according to him, not the cause of the depression of growth in such cultures. The assimilation of nitrogen from nitrates takes place by means of a reduction of the nitrates to nitrites, as in bacteria and the higher plants. Since nitrites are not stable in acid solutions, it is necessary to keep the cultures neutral or alkaline to show the formation of nitrites. In such cultures nitrites resulting from the reduction of nitrates were shown to occur.

KOSSOWICZ[17] examined a number of fungi with reference to their ability to obtain nitrogen from calcium nitrid supplied in a nutrient solution containing per liter 2.5 gms. dipotassium hydrogen phosphate, 0.5 gms. magnesium sulphate, 25 gms. cane sugar, and 5 gms. tartaric acid. The calcium nitrid was added after sterilization. The fungi used were *Botrytis bassiana*, *Penicillium crustaceum*, *P. brevicaule*, *Mucor Boidin*, *Cladosporium herbarum*, *Phytophthora infestans*, *Aspergillus glaucus*, *A. niger*, *Isaria farinosa*, and a species of *Fusisporium*. Of these only *Phytophthora infestans*, *Botrytis bassiana*, and *Mucor Boidin* showed any growth after three months. *Phytophthora infestans* caused the production of ammonia in the culture medium, but in the cultures of the other two fungi ammonia could not be detected with Nessler's reagent. The poisonous effect of calcium nitrid was shown by the feeble growth of the foregoing fungi on solutions containing calcium nitrid and ammonium chloride compared with their growth on solutions containing ammonium chloride alone as a source of nitrogen.

The availability of different phosphorus compounds as sources of phosphorus for *Aspergillus niger* has been studied by DOX.[18] Of the inorganic compounds he finds that orthophosphate, pyrophosphate, and metaphosphate serve well as sources of phosphorus, while hypophosphite and phosphite containing trivalent phosphorus, while not toxic, do not supply phosphorus in an available form. Several organic substances containing phosphorus were found to be excellent sources of phosphorus for the mold. The substances tested were phytin, sodium glycerinophosphate, sodium nucleinate, lecithin, casein, and ovovitellin. The author suggests that in all these cases phosphoric

[16] RITTER, G. E., Ammoniak und Nitrate als Stickstoffquelle für Schimmelpilze. Ber. Deutsch. Bot. Gesells. **29**:570–577. 1911.

[17] KOSSOWICZ, A., Über das Verhalten einiger Schimmelpilze zu Kalkstickstoff. Zeitschr. Gärungsphysiologie **1**:124, 125. 1912.

[18] DOX, A. W., The phosphorus assimilation of *Aspergillus niger*. Journ. Biol. Chem. **10**:77–80. 1911.

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acid is first split off from the organic compound by means of enzymes. This suggestion is strengthened by the facts that IVANOFF has prepared an enzyme from this mold which decomposes nucleic acid with the liberation of phosphoric acid, and the author himself has shown the presence in another mold of an enyzme capable of hydrolyzing casein.—H. HASSELBRING.

Current taxonomic literature.—O. AMES (Phil. Journ. Sci. Bot. **7**:1–27. 1912) in continuation of his studies in the Orchidaceae has published 27 new species of orchids from the Philippine Islands.—O. BECCARI (Pomono Coll. Journ. Ec. Bot. **2**:253–276. 1912) under the title "Palms indigenous to Cuba I" recognizes 14 genera, 3 of which are treated in detail in the present paper. One new species is added to the genus *Oreodoxa*, namely *O. princeps*. —C. H. BISSELL and M. L. FERNALD (Rhodora **14**:91, 92. 1912) record a new variety of *Lespedeza* (*L. capitata* var. *stenophylla*) from Illinois and Connecticut. G. BITTER (Rep. Sp. Nov. **10**:489–501. 1912) places on record supplementary data to his recent monograph of the genus *Acaena* and includes descriptions of new varieties from Central and South America. The same author (*ibid.* 529–565) under the title "Solana nova vel minus cognita I" has published 36 new species of *Solanum* also from Central and South America.—S. F. BLAKE (Rhodora **14**:102–106. *pl. 94.* 1912) characterizes several new forms of *Peltandra virginica*.—E. BRAINERD (Bull. Torr. Bot. Club **39**:85–97. *pls. 5–7.* 1912) presents an interesting article on "Violet hybrids between species of the *palmata* group," recording several new hybrids in the genus.—A. BRAND (Univ. Calif. Pub. Bot. **4**:209–227. 1912) presents a preliminary consideration of the Hydrophyllaceae of the Sierra Nevada region. Several new varieties and forms are described and certain changes in nomenclature are made. The same author (Phil. Journ. Sci. Bot. **7**:29–36. 1912) records the results of further investigations on the Symplocaceae of the Philippine Islands, adds 3 new species to *Symplocos*, and gives a revised key to the 26 recognized Philippine species of this genus.—T. S. BRANDEGEE (Univ. Calif. Pub. Bot. **4**:269–281. 1912) under the title "Plantae Mexicanae Purpusianae IV" has published 29 new species and 2 varieties of flowering plants. One new genus (*Oxyrhynchus*) of the Leguminosae is proposed.—H. BRAUNS (Verhandl. K. K. Zoolog.-Bot. Gesell. Wien **61**:139–143. 1911) describes 6 new species of *Nitella*, 2 of which are from Costa Rica.—J. BROADHURST (Bull. Torr. Bot. Club **39**:257–278. *pls. 21, 22.* 1912) under the title "The genus *Struthiopteris* and its representatives in North America" gives a revision of the genus, recognizing 9 species, of which 2 are new to science.—J. BURTT-DAVY and R. POTT-LEENDERTZ (Ann. Transvaal Mus. **3**:119–182. 1912) have issued a check list of the flowering plants and ferns of the Transvaal and Swaziland. Approximately 3240 species are enumerated, representing 920 genera and 157 families.—E. J. BUTLER (Ann. Botany **25**:1023–1035. 1911) describes and illustrates a new genus and species (*Allomyces arbuscula*) of the Leptomitaceae from India.—E. CLAASSEN (Ohio Nat. **12**:543–548. 1912) records about 125 species and varieties of lichens from

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northern Ohio.—F. S. COLLINS (Tufts Coll. Studies Sc. Ser. 3:69–109. *pls. 1, 2.* 1912) in a supplementary paper on "The green algae of North America" records important data on this group of plants and adds several new species, varieties, and forms.—E. B. COPELAND (Philip. Journ. Sci. Bot. 6:359–364. 1911) under the title of "Cyatheae species novae orientales" has published several new to science. The same author (*ibid.* 7:47–68. 1912) makes important contributions to our knowledge of the fern flora of the Philippines and describes 29 species new to science.—H. N. DIXON (Journ. Bot. 50:145–156. *pl. 517.* 1912) in continuation of his studies of the mosses of India has published jointly with CARDOT several species new to science and proposes a new genus (*Bryosedgwickia*) of the Entodontaceae.—A. D. E. ELMER (Leafl. Philip. Bot. 4:1475–1520. 1912) has described 40 new species of flowering plants from the Philippine Islands.—A. W. EVANS (Bull. Torr. Bot. Club 39:209–225. *pls. 16, 17.* 1912) in continuation of studies in the Hepaticae of Puerto Rico describes and illustrates a new species and variety of *Diplasiolejeunea*.—H. S. FAWCETT (Phytopathology 2:109–113, *pls. 8, 9.* 1912) has published an account of a new fungus (*Phomopsis citri*) which is said to cause the so-called stem-end rot of citrus fruits.—W. FAWCETT (Journ. Bot. 50:177–182. *pl. 518.* 1912) has published 9 new species of *Pilea* and a new *Peperomia* from Jamaica. —F. FEDDE (Rep. Sp. Nov. 10:478–480. 1912) in continuation of his studies on the genus *Corydalis* records 2 new species and a new variety from western and southwestern United States.—M. L. FERNALD and K. M. WIEGAND (Rhodora 14:115, 116. 1912) record a new variety of *Carex* (*C. scoparia* var. *subturbinata*) from Newfoundland, etc.—H. M. HALL (Univ. Calif. Pub. Bot. 4:195–208. 1912) under the title "New and noteworthy Californian plants I" records important notes on plants of the region indicated and makes several new combinations as the result of field and herbarium study.—R. HAMET (Notizblatt 5:277, 278, 1912) has published a new species of *Sedum* (*S. Adolphi*) based on plants cultivated in the Royal Botanical Garden at Dahlem-Steglitz from seeds collected in Mexico by PURPUS.—L. L. HARTER and E. C. FIELD (Phytopathology 2:121–124. 1912) under the title "*Diaporthe*, the ascogenous form of sweet potato dry rot" describes a new species (*Diaporthe batatatis*).—A. HEIMERL (Oesterr. Bot. Zeitschr. 51:10, 11. 1911) has published a new species of *Hilleria* (*H. longifolia*) from Peru.—A. A. HELLER, (Muhlenbergia 8:49–58. 1912) describes a new species of *Castilleja* (*C. lapidicola*) and raises the sectional name *Siphonella* Gray to generic rank, citing *Gilia Nuttallii* Gray as the type of the proposed genus. The same author (*ibid.* 61–71) in continuation of his studies in the genus *Lupinus* describes two new species from Oregon.—F. HEYDRICH (Bib. Bot. Heft 75, pp. 1–21, *pls. 1, 2.* 1911) has proposed the generic name *Crodelia* to which is transferred *Lithophyllum incrustans* Phil. Some 25 forms of this species are indicated under the new combination.—J. HUTCHINSON (Kew Bull. 1912. 223, 224) has published a new *Sapium* (*S. cladogyne*) from British Guiana.—A. KNEUCKER (Allgem. Bot. Zeits. Beilage zu Jahrgang. 1911. pp. 12) has described 3 new species in the Cyperaceae from

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the Philippine Islands.—K. KRAUSE (Notizblatt **5**:264, 265. 1912) records 2 new species of *Phoradendron* from Costa Rica. The same author (*ibid.* 266, 267) has published 2 new species of Araceae from the Philippines.—F. D. LAMBERT (Tufts Coll. Studies Sci. Ser. **3**:111–115, *pl. 3.* 1912) describes and illustrates a new genus and species of alga (*Didymosporangium repens*) of the Chaetophoraceae, found on *Antithamnion plumula* at Naples, Italy.—H. LÉVEILLÉ (Bull. Geogr. Bot. **21**:149. 1911) has published a new species of *Epilobium* (*E. Arechavaletae*) from Uruguay.—J. M. MACFARLANE (Contr. Bot. Lab. Univ. Penn. **3**:207–210. *pls. 1, 2.* 1911) has published 2 new species of *Nepenthes* (*N. Merrilliana* and *N. truncata*) from the Philippine Islands.—B. MACKENSEN (Bull. Torr. Bot. Club **39**:289–292. 1912) records 3 new species of *Opuntia* from Texas.—J. H. MAIDEN (Rev. Euclayptus **2**, parts 4–6. pp. 135–216. *pls. 61–72.* 1912) contains descriptions, notes, and illustrations of several different species of *Eucalyptus*.—G. MASSEE (Kew Bull. 1912. 189–191) has described several now species of fungi, including one (*Eutypa gigaspora*) from Trinidad.—E. D. MERRILL (Phil. Journ. Sci. Bot. **7**:71–107. 1912), under the title "Sertulum Bontocense" has described 32 new species of flowering plants from the Island of Luzon, P.I., and proposes a new genus (*Vanoverberghia*) of the Zingiberaceae. The same author (*ibid.* **6**:369–406) presents a synoptical revision of the Philippine species of *Begonia*, recognizing 59 species of which 33 are described as new.—B. NĚMEC (Bull. Int. Acad. Sci. Bohême **16**:67–84. *pls. 1, 2.* 1911) under the title "Zur Kenntnis der niederen Pilze I. Eine neue Chytridiazee" presents a detailed account of a fungus to which he gives the name *Sorolpidium Betae*, nov. gen. et sp.—R. PILGER (Nobizblatt **5**:259–263. 1912) has published 10 new species of *Plantago* from America.—L. RADLKOFER (Phil. Journ. Sci. Bot. **6**:365–367. 1912) proposes a new genus (*Hebonga*) of the Simarubaceae from the Philippine Islands; the genus is represented by two known species.—C. S. SARGENT (Pub. Arnold Arb. No. 4, pp. 145–312. 1912) in cooperation with E. KOEHNE, A. REHDER, C. SCHNEIDER, and E. H. WILSON under the leading title of "Plantae Wilsonianae" has issued the second part of a series of papers dealing with plants collected in western China by Mr. E. H. WILSON in 1907, 1908, and 1910. The paper contains many new species and varieties, particularly in the Saxifragaceae and Rosaceae.—W. A. SETCHELL (Univ. Calif. Pub. Bot. **4**:229–268. *pls. 25–31.* 1912), under the title "Algae novae et minus cognitae I" has published several new species, and proposes the following new genera: *Hapterophycus* of the Ralfsiaceae, *Besa* of the Gigartinaceae, and *Baylesia* of the Dumontiaceae.—J. M. GREENMAN.

The evolution of the chalazogams.—A rather extended paper by NAWASCHIN and FINN[19] describes the morphology of *Juglans nigra* and *J. regia* and discusses the significance of chalazogamy. The paper is in Russian,

[19] NAWASCHIN, S., and FINN, W., Zur Entwickelungsgeschichte der Chalazogamen. *Juglans nigra* und *J. regia*. Mem. Soc. Nat. Kieff **22**:1–85. *pls. 1–4.* 1912.

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but there is a summary in German, the principal features of which are as follows: Among the seed plants there is an evident tendency to reduce the male gamete so that the male cytoplasm does not take part in fertilization. In this reduction the binucleate generative cell has played an important part. Its appearance in the gymnosperms (Abietineae, some Taxaceae, Gnetales) is accompanied by a constantly increasing disorganization of the male cytoplasm, which finally leads to the naked sperm nuclei of the higher angiosperms. The species of *Juglans* studied have binucleate generative cells which reach the embryo sac without disorganization, and correspond exactly to the binucleate generative cells of certain gymnosperms. In this feature, therefore, these species occupy an intermediate position between gymnosperms, in which the cytoplasm reaches the egg cell, and the higher angiosperms, in which the male cytoplasm disorganizes in the pollen tube or even in the pollen grain.

The persistence of the male cytoplasm in *Juglans* is thought to be a primitive character retained from their gymnosperm ancestors, and the appearance of this character in chalazogams is said to be significant and is a further proof of the great age of these plants. The tendency in seed plants to reduce the male gametes seems correlated with the appearance of the pollen tube, for the simplification of the male gametes goes hand in hand with the evolution of the pollen tube.

While some of these conclusions seem rather arbitrary, the progressive reduction of the male gametes is a fact which all must recognize. Criticisms are left for those who can read the full paper.—CHARLES J. CHAMBERLAIN.

Winter condition of brown rots.—Conflicting and uncertain statements n the literature regarding the manner in which the fungi producing the brown rots of stone-fruits and pomaceous fruits live through the winter have led EWERT[20] to study the behavior of the conidia of these fungi with regard to their capacity for persisting through the winter. The rarity of the apothecia makes it improbable that these play an important part in maintaining the brown rot fungi.

EWERT finds that the two species of brown rot fungi, *Monilia cinerea* and *Monilia fructigena*, differ radically in their mode of passing the winter, a fact which may account for the discrepancies in the literature, since most of the conflicting statements regarding the persistence of the spores during winter were made before WORONIN had shown that the two species are clearly distinct. EWERT finds that the conidia of *Monilia cinerea*, which occurs primarily on stone-fruits but which can also infect pomaceous fruits, are capable of germinating at any time during the winter. They persist during the winter in the spore-cushions on mummies of cherries, plums, and other stone-fruits, and also on pomaceous fruits if these happen to be infected. Exposure to tempera-

[20] EWERT, E., Verschiedene Überwinterung der Monilien des Kern- und Steinobstes und ihre biologische Bedeutung. Zeitschr. Pflanzenkrank. 22:65–86. 1912.

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tures much lower than those which occur annually at PROSKAV, where the investigations were made, did not injure the germinative capacity of the spores. The mycelium also remains alive and produces new spore-cushions in the spring.

The conidia of *Monilia fructigena*, which occurs chiefly on pomaceous fruits, lose their capacity for germination very early in the winter. The fungus persists solely by means of the mycelium. New spores are produced in the spring, when the mummies covered with the crust-like spore-cushions are soaked and kept in a warm place.

The twig-blight of stone-fruits, which flower early in the season, is caused entirely by *Monilia cinerea*, whose spore-cushions are produced much earlier than those of *M. fructigena*. The spores of *M. fructigena* are not formed at the flowering time of the stone-fruits.—H. HASSELBRING.

Ecology of mosses.—A careful study of the mosses of Isle Royale, Mich., by COOPER[21] proves that there is a well marked succession extending from pioneer conditions to the establishment of the climax forest. From beginnings both upon the rock shore and in the bogs two distinct lines lead to the same climax, characterized by *Calligeron Schreberi*, *Hylocomium proliferum*, and *Hypnum cristacastrensis* as dominant species. The importance of mosses as pioneers upon bare rock surfaces and in peat bogs has long been recognized, but the present study shows that they are of equal importance in the climax forest in promoting the accumulation of humus and in the conservation of soil moisture. This investigation represents a new departure in the field of ecology, and proves not only that the same general laws of succession hold among bryophytes as among seed plants, but that these plants of lower rank may often serve as indicators of the advancement attained by any particular forest association. This latter feature may prove of the greatest value in the study of our northern forests, where the number of tree species is reduced to a minimum.—GEO. D. FULLER.

Calcium-magnesium ratio.—LOEW[22] calls attention to the fact that the results obtained by MEYER and LEMMERMAN in their work on the calcium-magnesium ratio do not agree with those previously worked out by himself. He claims that the results obtained by them were due to the fact that the soi was insufficient in amount for the number of plants grown. The dry weight of their plants was only half the weight of plants grown under ordinary conditions. This dwarfing was due to the arresting of root growth, and no conclusion can be drawn concerning the calcium-magnesium ratios from plants grown under crowded conditions.—JOHN N. MARTIN.

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[21] COOPER, WILLIAM S., The ecological succession of mosses as illustrated upon Isle Royale, Lake Superior. Plant World 15:197–213. 1912.

[22] LOEW, OSCAR, Über angebliche Widerlegung der Lehre vom Kalkfaktor. III. Landwirtschaftl. Jahrb. 42:181–192. 1912.

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VOLUME LV NUMBER 2

THE
BOTANICAL GAZETTE

FEBRUARY 1913

THE MORPHOLOGY OF ARAUCARIA BRASILIENSIS

I. THE STAMINATE CONE AND MALE GAMETOPHYTE

L. LANCELOT BURLINGAME

(WITH ELEVEN FIGURES AND PLATES IV AND V)

Introduction

Although wood of the araucarian type, strikingly resembling that of the ancient Cordaitales, has been known for a long time and has been used as evidence of the antiquity of the araucarians and as a proof of their relationship to the Cordaitales, both of these opinions have been vigorously challenged. It has been asserted that they are less ancient than the Abietineae and are derived from them (**7, 9**); that possibly they are not related to other gymnosperms at all and have been derived from a lycopod ancestry (**17, 18, 20**); that "the geological claim for the great antiquity of the Abietineae thus fails on critical study of the two forms upon which it is based" (**27**); that "the ancient geological and widely separated geographical distribution (of Araucarineae), the large microsporangiate cones in comparison with the megasporangiate cones, the evident transition between the sporophylls and the foliage leaves are indications of an interesting and probably primitive group. The anatomy of the microsporophylls and megasporophylls indicates that they are homologous structures, functionally differentiated" (**26**); that "unfortunately, no teratological phenomena, on which he always laid great stress, were known in the *Araucariae*, but they were in the Abietineae and showed that

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the single ovule was a modification of an axillary shoot bearing sporangia" (30, 31).

In the face of opinions so diverse, the desirability of additional facts is very evident. We know already that the pollen grains and pollen tubes of *Araucaria* contain numerous nuclei, most of which are prothallial or vegetative (13, 24, 25, 26), and that the same condition obtains in *Agathis* (24), with the added information that there are definitely "two large male nuclei" (6). Among the Podocarpineae the same conditions are known to be true for *Podocarpus* (1, 2, 5, 8, 22, 33), *Dacrydium* (8, 23, 32, 33), *Phyllocladus* (11, 33), *Saxegothaea* (15, 29), and *Microcachrys* (28). The present investigation was undertaken in the belief that additional knowledge of the morphology of the Araucarineae would aid very materially in clarifying our ideas concerning the origin (or origins) of Coniferales and the relationship of the Pinaceae, particularly the Abietineae, and the Podocarpineae (and Taxaceae generally).

The materials for this investigation have been secured through the kindness of Mr. JAMES C. FLOOD of San Francisco, California, from his country place, Linden Towers, at Menlo Park, California, to whom the writer wishes to express his sense of obligation and appreciation. He is also under obligation for actual assistance in making the collections to the generous assistance of Mr. ROACH, the gardener at Linden Towers, to whom also his thanks are due. Collections were begun in March 1910 and made weekly up to the middle of November, when they were interrupted by illness until February 1911. Collections were again made from November 15, 1911, to February 1912, thus completing the series.

Various killing and fixing agents have been tried. A solution recommended by JUEL (10) gave as satisfactory results as any for most stages. Flemming's stronger solution, as well as the chrom-acetic mixture recommended in CHAMBERLAIN's *Methods in plant histology*, also gave good results for some stages, but fails to penetrate the microsporangium during the development and division of the mother cells, owing partly to the nearly impervious epidermis that develops about this time, and partly, perhaps, to the presence then in the pollen sacs of a sort of mucilage, apparently produced by the

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degeneration of the walls of the mother cells. At certain times in mid-winter practically all stages of the cones are present on the trees at the same time. Notwithstanding the fact just mentioned, stages between the prophase of the mother cell and tetrads were collected only four times, though diligently sought for. The same is true of the stages in the development of the gametophyte from mature microspores to those in which the primary spermatogenous

FIG. 1.—Forest of *Araucaria brasiliensis* on the Rio Tibagy, State of Parana, southern Brazil.—Photograph by J. C. BRANNER.

cell has already divided. The reasons for this state of affairs are not very apparent, though it may be that these stages are passed through very rapidly or that division occurs during the night.

The habit of the tree is shown in text fig. 1, representing old trees in their native habitat, and in text fig. 2, an ovulate tree from the gardens at Linden Towers.

The staminate cone

Among the numerous specimens of *Araucaria* in these gardens, belonging to at least four different species, there are three staminate

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ones of *A. brasiliensis*. They are about 30 years old and range in height from 25 feet to about 60 feet. The largest one is about 20 inches in diameter. Most of the collections were made from the smallest tree because it has had the crown broken out, and on this account fruits much nearer the ground, a matter of some

FIG. 2.—Ovulate tree from gardens at Linden Towers, showing retention of lower branches in young trees.

consequence when one considers ways and means of securing cones from a "monkey puzzle" tree. This tree was selected for the additional reason that the range of stages on it at any time was greater. It had moreover the peculiarity of forming its cones much earlier in the fall and continuing to form new ones later in the

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spring. Numerous collections were made from one of the other trees in order to make sure that development in the cones from all the trees was the same.

FIG. 3.—Staminate branch of *A. brasiliensis* bearing two old cones of previous season and several young ones; note the new shoot from one of the old cones.

In the fall (August to October) one finds the shoots of *A. brasiliensis* tipped with terminal buds, in some of which, distinguished by being larger and plumper, one can find the very young cones. As soon as the branch has developed from such a bud, one

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usually finds about 3–6 staminate cones scattered along the new shoot (text fig. 3). Each cone terminates a short leafy branch, which may occasionally continue its growth the following season, but usually the cone dries up, turns brown, and falls off the winter following the shedding of its pollen (text fig. 3). The mature cones are very large, immediately after having shed their pollen being frequently as much as 15 cm. long and 3 cm. in diameter; they are about one-third smaller before shedding. Text fig. 4 shows an unopened cone, a cone shedding its pollen, and the apical view of a mature cone broken in two, about natural size. Such a cone as is shown in the photograph has about 1000 sporophylls, disposed in about 12 spiral rows, each of which makes 2 or 2.5 turns. There are usually 10–15 sporangia, pendent (text figs. 5 and 6) from the expanded distal portion of the sporophyll on its morphologically abaxial side. Each sporangium contains 500–1000 pollen grains. A little calculation will show that the output of a terminal bud may easily reach a billion pollen grains. The pollen is shed in the spring from the first of April to the latter part of May for the most part, although I have found cones shedding in December and as late as July 1. The sporangia dehisce through longitudinal slits on the sides of the sacs facing the other row of sporangia, so that the pollen is shed into the space between the inner and outer rows of sporangia.

By dissecting the terminal buds already referred to, one can recognize the young cones when they are merely rounded growing points. Each one is enveloped in two or three layers of delicate leaves and is slightly flattened on the side next the main axis of the bud. Plate fig. 1 shows a slightly older cone, on which the first sporophylls are forming. A sporophyll is first recognizable as a group of meristematic cells (plate fig. 2) just beneath a slight emergence of the smooth surface of the growing point (plate fig. 1). This emergence increases in size rapidly by growth throughout. Very soon its distal end expands until the whole structure somewhat resembles a mushroom with a very short stalk and one-half of the pileus removed. The stalk is so short that the abaxially placed swollen portion of the sporophyll is in contact with the cone axis. From its surface grow the sporangia, elongating toward the cone

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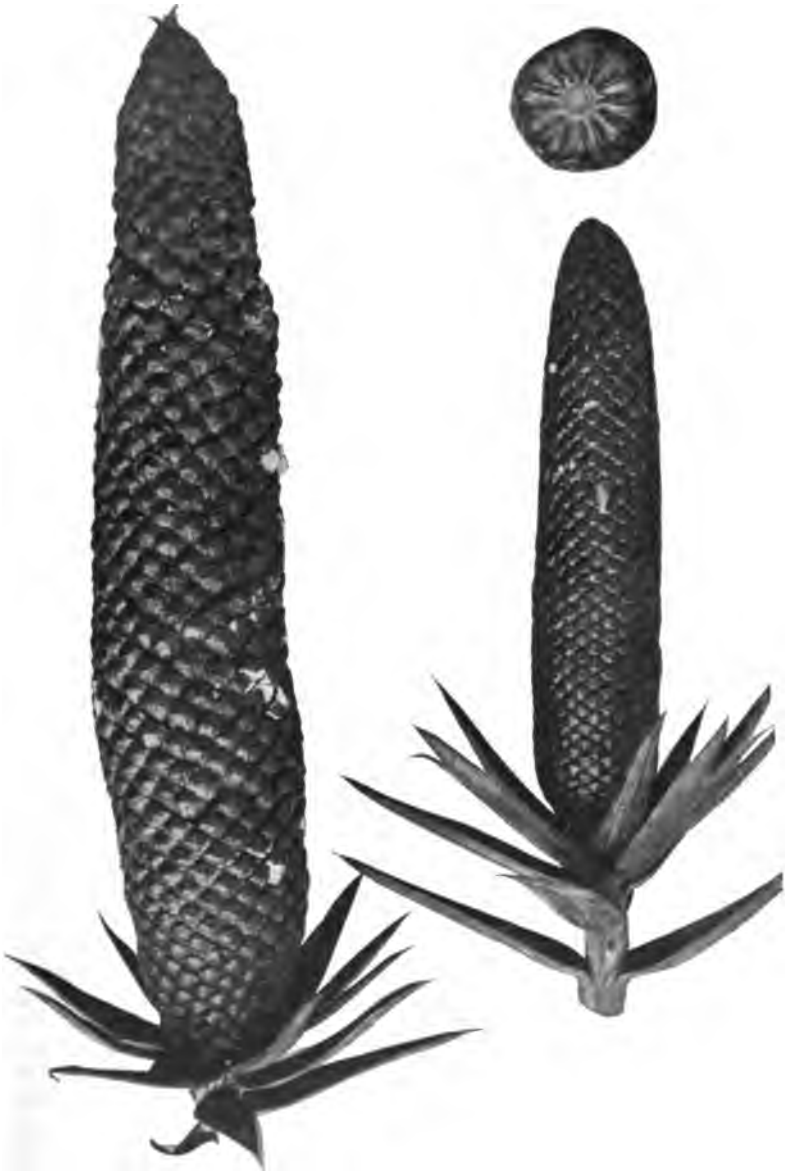

FIG. 4.—Cone shedding pollen (to right), mature unopened cone, and cross-section of mature cone; natural size.

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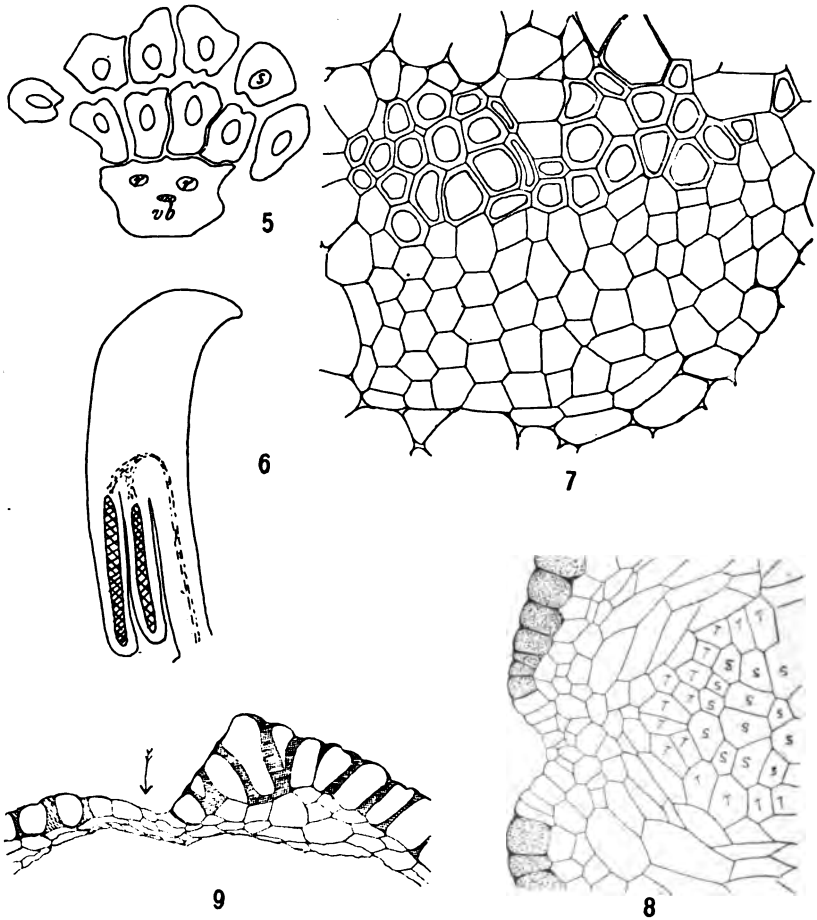
axis as fast as the axis of the sporophyll itself elongates. Like the sporophyll itself, the sporangia are first distinguishable as meri-



FIGS. 5–9.—Fig. 5, cross-section of sporophyll, showing relation of sporangia to one another and to the stalk; fig. 6, longitudinal section of a sporophyll, showing position of sporangia and course of their vascular supply; fig. 7, cross-section of a vascular bundle of sporophyll; fig. 8, cross-section of a sporangium at mother cell stage, showing sporogenous cells (*s*), tapetal cells (*t*), 4–6 layers of wall cells, tannin-filled epidermal cells, and thin cells where dehiscence will take place; ×250.; fig. 9, annulus and stomium just before dehiscence; ×250.

stematic outgrowths consisting of several cells. Plate fig. 3 shows part of three sporangia adjacent to one another in the same row, and plate fig. 4 shows a section at right angles to it, showing the

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beginnings of two sporangia adjacent to one another but in different rows.

Occasionally one can distinguish what appears to be the archesporium almost as soon as the sporangium itself is recognizable, but much more commonly it cannot be detected until the sporangium is 12–15 cells in length and 8–10 cells wide (plate figs. 4, 5, 6). Not infrequently sporangia as far developed as that shown in plate fig. 7 do not show any differentiation of sporogenous cells. Ordinarily one can recognize all the primary regions of the sporangium at this stage. The cells of the tapetum seem to be derived more or less indifferently from those of the wall layers outside, or from derivatives of the inner and presumably sporogenous cells. However, I should not like to be too dogmatic in regard to this. Multiplication of cells continues until the sporogenous tissue consists of a mass some 20 cells in cross-section (plate fig. 8) and 40–50 cells long. The tapetum remains one or two cells thick, the ultimate cells being elongated radially and retaining their position and structure till some time during the development of the male gametophyte. At this time there are 4–6 layers of wall cells radially flattened, with very little cell contents. The epidermis is at this time filled with a densely staining substance, resembling tannin in its staining reactions, and presenting a very effective barrier to the ready penetration of the ordinary reagents. In the further development of the sporangium the contents of these epidermal cells disappear, and the radial walls, seen in a cross-section of a sporangium, thicken in the fashion of a fern annulus, except at the point of future dehiscence. The wall cells are eventually crushed and more or less destroyed and the tapetum finally disintegrates (text figs. 8 and 9).

Sporogenesis

After the last division of the sporogenous cells, the mother cells begin enlarging, until at the prophase of the heterotypic division they have attained a diameter more than twice that of the sporogenous cells. This eight or ten times increase of volume is largely water, the cytoplasm becoming greatly vacuolated as the growth increases. There is a corresponding enlargement of the nucleus,

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though not proportionally so great (plate fig. 9). Once this increase in size has been effected in the mother cells and their walls, the cell contents appear to round up and shrink away from the walls more or less; just how much I am unable to say owing to the difficulty of determining whether part or all of the shrinkage may not be due to the difficulties of securing satisfactory fixation. The walls themselves have a tendency to persist until after the young spores have been formed, but apparently they change their chemical condition and become more or less mucilaginous in character. Sometimes no walls at all are visible, but the spaces among the mother cells are filled with a thin sort of mucilage. The greater the amount of this mucilage present, the poorer the fixation.

Owing to the difficulties already mentioned, I have but little trustworthy information concerning the course of events during the reduction divisions. Stages in the formation of the presynaptic spireme, synapsis, and diakinesis were observed. At the metaphase of the heterotypic division there are 8 bivalent chromosomes, but the material did not permit one to follow the method of their formation. The spindle fibers are attached to their apices (plate fig. 11), and they are drawn apart as short stubby masses and collect at the pole in a close mass. They appear at the spindle of the homeotypic division as much longer rods curved into more or less U-shaped chromosomes. No walls are formed, apparently, until after the spore nuclei have passed into the resting condition, when a system of fibers is present between the nuclei, on which the plasmatic membranes separating the young spores arise (plate figs. 13 and 14).

The young spores now form walls around themselves, entirely within the old mother cell wall if it is still present. The spores then begin a slow enlargement and thickening of the walls. At first the growth consists merely in enlargement of the wall without any apparent increase of cytoplasm or nucleus. There is either one very large vacuole almost entirely filling the spore or many smaller ones separated by only the most tenuous cytoplasmic walls. At this time no inclusions of starch or other food materials are visible. After the spore wall has reached its mature size, but not final thickness, the cytoplasm becomes more abundant and the nucleus enlarges (plate figs. 16 and 17). In the large nucleus there is a large

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nucleolus and rather scanty chromatin. From this is organized a rather long, loose spireme, apparently containing scanty chromatin. It segments to form 8 chromosomes, which contract into rather small dense oval masses (plate fig. 18).

Male gametophyte

The results of this first division are a primary prothallial cell and a free nucleus (plate fig. 19). The latter at once divides to produce a second prothallial cell, which takes its place over the preceding. The next division yields the free tube nucleus and the primary spermatogenous cell (plate fig. 21). Meantime the prothallial cells have divided (plate figs. 20, 21, 22). The primary spermatogenous cell now divides, yielding the usual stalk and body cell. The stalk cell is very evanescent, usually becoming confused with the general cytoplasm very quickly. Plate fig. 25 shows one of the few preparations in which it could still be distinguished as a distinct cell. Another interesting case was observed in which there seemed to be two free and equal cells in the unshed pollen grain. The usual condition of a mature pollen grain, with 15–25 free prothallial nuclei, a recognizable tube nucleus, and a single body cell, is shown in plate fig. 27.

It is in this condition that the pollen is shed in April (usually). The potential number of pollen grains is four to eight times as great as the actual number formed. It has already been remarked that the ordinary number of mother cells is about 1000, while the usual number of pollen grains that mature in a sporangium is only 500–1000. At the time they are shed the pollen grains have a two-layered wall, the outer coat of which easily separates from the inner (plate figs. 25, 26, 27), but which does not appear to do so naturally to form wings. At the time they are shed they contain a great many very large starch grains, a few of which are shown in plate fig. 27. They are usually so crowded with it that the microtome knife scatters the contents all about in cutting sections of shed pollen.

Pollination

The ovulate cones are first recognizable in late April. At this time there is no trace of ovules on the scales and the pollen lodges somewhere near the free edge of the so-called ligule (text fig. 10).

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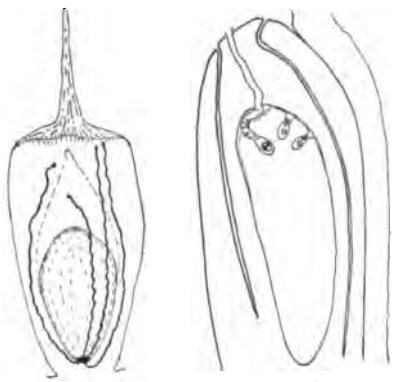
Whether the pollen shed in the early part of the season finds a lodgment in a position to become effective is uncertain. Neither does there appear to be any available data as to whether this precocious shedding of pollen occurs in its native habitat. Though California and Brazil exhibit a somewhat rough correspondence in their seasons of rainfall and plant growth, yet it is probably not sufficiently exact to permit of any very satisfactory inferences as to the corresponding behavior in the two habitats.



FIGS. 10, 11—Fig. 10, ovule and scale in December, showing course of pollen tubes; fig. 11, course of pollen tube through nucellus to archegonium.

I have not yet ascertained certainly how long a time elapses after the pollen falls on the scale before germination occurs. Grains that have germinated can be found in the latter part of summer after the fogs have set in. Meantime during the summer the ovule is forming and the stigmatic nucellus is usually ready to receive the advancing pollen tubes some time in September or October.

I have not so far succeeded in germinating pollen to any very advanced stage, nor have I been able to follow with any certainty the course of events in the pollen tube before it reaches the nucellus. When the ovuliferous scales are pulled apart, very numerous pollen tubes are usually found sewed back and forth between the two adjacent surfaces of the scales. One can sometimes isolate one without completely destroying it, but I have learned from such preparations nothing more than that there are numerous nuclei and a body cell present. One could infer that they would be there, inasmuch as they were in the pollen grain, and they are afterward present in the tube when it enters the nucellus. Whether division of the prothallial nuclei occurs in the tube or not is uncertain, owing to the fact that I have never been able to obtain an entire tube in which I

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could count the nuclei and be sure of having seen them all. These nuclei do increase markedly in size, and much of the starch which entered the tube at germination disappears before penetration of the tube into the nucellus.

At the time that the tube enters the nucellus there are numerous nuclei and the body cell present. I was unable to distinguish the tube nucleus any longer from the others. At first only a few of these nuclei enter the portion of the tube in the nucellus. The body cell is usually in that portion just outside of the nucellus or just barely within it. There is apparently very little activity in the development of the tube from the time it first penetrates the nucellus for a short distance until spring. I did not succeed in finding the mitosis concerned in the division of the body cell, though the two male cells were found two or three times still imbedded in a common mass of dense cytoplasm. The two nuclei frequently differ in size markedly. The body cell and its nucleus have increased in volume after leaving the pollen grain some six or eight times by the time the pollen tube has penetrated the nucellus in October (plate fig. 28). This increase continues on an even greater scale up to the time of division. After the division of the body cell, one, at least, of the pieces organizes itself into a large male cell or perhaps a real sperm. These vary considerably in size and in the definiteness of their organization. They all agree in being very large and in being more or less completely delimited from the cytoplasm in which they are imbedded (plate fig. 29). Almost invariably the large nucleus is at the extreme end of the cytoplasm and the cytoplasm is very often evidently arranged in such a way as to lead one to surmise that the nucleus actively changes its position in reference to the cytoplasm. The nucleus is invariably at that extremity which would lead in the direction that the "sperm" would be inferred to be moving. The cytoplasmic body is sometimes bent, almost at a right angle in one instance observed, in such a way as to remind one strongly of the creeping movements of an amoeba. In one instance of two "sperms" lying in a common mass of cytoplasm, apparently having just divided, there was present a peculiar fibrillar structure reminding one of a nuclear spindle without the chromosomes and with an aster at either pole. Whether this is

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an indication of the presence of a blepharoplast and whether the "sperm" is actually motile, I hope to be able to ascertain during the coming spring. The division probably occurs in the latter part of February and in the part of the tube outside of the nucellus.

During this time the pollen tube has advanced through the nucellar tissues in a more or less irregular and branching course. When it reaches the upper part of the female gametophyte it usually turns aside from the apex, which is protected by a cap of crushed nucellar cells, and creeps laterally along the surface of the gametophyte until it reaches the narrow opening leading down to one of the archegonia, down which it descends to the neck of the archegonium. Here it becomes perforated. The "sperm" passes through the opening and crowds the neck cells of the archegonium apart without destroying them, and plunges down into the egg so vigorously as to leave a very distinct wake behind it in the cytoplasm. Fertilization occurs in the latter part of March or first week or two of April.

Discussion

It is not proposed at this time to enter into any general discussion regarding the broader questions that prompted the investigation, but to let that await the issue of further investigation of other phases of the life history of this species and of the other three species of which material is available. However, it may not be amiss to point out that this added information concerning the male gametophyte goes far toward inducing a belief in the primitive condition of the araucarians. It certainly strengthens the resemblance to the podocarps and tends to increase our confidence in their genetic connection. Barring the abnormally large "sperms" of *Araucaria* and the greater number of prothallial nuclei, its male gametophyte exhibits an almost identical structure even in small details with that of the Podocarpineae. On the contrary, it is clear that the type of male gametophyte found in these two tribes is essentially different from that found in *Cupressus Goveniana* (10) and *Juniperus communis* (14). In these we have a multiplication of spermatogenous cells, which may be induced, as has been suggested, by the opportunity for more than one sperm to function, but in any case is doubtless a reversion to an ancient habit (10, 14). This view

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is strengthened by the occurrence of more than two sperms in *Microcycas* (3) and *Ceratozamia* (4). The deposition of the pollen at a distance from the nucellus has also been recorded for *Saxegothaea conspicua* (15), and serves to strengthen the likeness of the araucarians and podocarps.

By long odds the most interesting and suggestive feature of the male gametophyte of the araucarians yet known is the remarkably large "sperms" and the possibility of their motility. The one figured (plate fig. 29) is about 150 μ long. It is by no means the largest one observed, but seemed to be the one most definitely organized. Such dimensions are only known elsewhere among the actively swimming sperms of the Cycadales and *Gingko*. It is of interest to note that the kauri (6) appears to have two large nuclei also, though it is not stated that they constitute part of organized cells. Inasmuch as *Agathis* has usually been held to be more primitive in most respects than *Araucaria*, it may be possible that they will yet be found there. The aster-like fibers found in the dividing body cell are of course very suggestive of a blepharoplast, and one might perhaps legitimately expect such structures to be found in connection with such large and possibly motile male cells. Again they might be only such structures as have been recorded by LAND (12) in the egg of *Ephedra*.

Summary

1. The staminate cones are extraordinarily large and have numerous sporophylls with an indefinite number of pollen sacs pendent from the abaxial side of the swollen apex.

2. An almost incomprehensibly great number of pollen grains is produced.

3. The method of differentiating the sporogenous tissue is variable and indefinite. The size of the sporangium and the number of microspores is subject to wide fluctuations.

4. The structures concerned in dehiscence are very fernlike.

5. The chromosome number in the male gametophyte is 8.

6. Prothallial tissue is formed in a manner almost identical with that in the Podocarpineae, but the number of cells so formed is greater.

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7. The pollen is shed with numerous prothallial nuclei, stalk nucleus, tube nucleus, and body cell free in it.

8. The pollen does not fall upon the nucellus but upon the ovuliferous scale at a considerable distance from the position of the ovule.

9. About a year elapses between pollination and fertilization.

10. No ovule has yet been formed on the scale at the time of pollination and the pollen tube does not reach the ovule for 5 or 6 months afterward.

11. The body cell is single, at least usually, and large.

12. Two male cells (sperms perhaps) are formed and are usually unequal.

13. There may be a blepharoplast-like body associated with the division of the body cell.

14. Fertilization occurs about the first of April.

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EXPLANATION OF PLATES IV AND V

All figures have been drawn under Zeiss apochromatic objectives and compensating oculars with the aid of a camera lucida. Figs. 2–8 were drawn with 4 mm. obj. and compensating ocular 6; figs. 9–27, under obj. 3 mm. and ocular 12; figs. 28 and 29, under 3 mm. obj. and compensating ocular 6.

Fig. 1.—Longitudinal section of a young cone from a terminal bud: *sc*, scale leaf; *sp*, young sporophyll; *vb*, vascular bundle; ×12.

Fig. 2.—Primordial meristem of very young sporophyll drawn from same cone as fig. 1; ×250.

Fig. 3.—Cross-section of a cone showing the sporangial meristems; ×250.

Fig. 4.—Longitudinal section of cone of same age as preceding: section passes through the stalk of the sporophyll and through the primordia of one sporangium in each row; *c.ax*, axis of cone; ×250.

Fig. 5.—Transverse section of cone and longitudinal section of sporangium: sporogenous tissue not defined; ×250.

Fig. 6.—Same as fig. 5, but showing usual differentiation of sporogenous tissue (*spt*); ×250.

Fig. 7.—Usual stage of differentiation of tapetum (*t*); ×250.

Fig. 8.—Cross-section of sporangium after last sporogenous division; ×250.

Fig. 9.—Somewhat shrunken mother cell showing eight times increase in volume; ×770.

Fig. 10.—Portion of a nucleus in which the heterotypic chromosomes are forming; ×770.

Fig. 11.—The 8 heterotypic chromosomes; ×770.

Fig. 12.—Second division of mother cell; ×770.

Figs. 13 and 14.—Tetrads, showing cell division; ×770.

Fig. 15.—A group of young microspores; ×770.

Figs. 16 and 17.—Mature microspores; ×770.

Fig. 18.—Division of microspore nucleus; ×770.

Fig. 19.—Showing first prothallial cell (*pc'*); ×770.

Fig. 20.—Mitosis of a prothallial cell; ×770.

Fig. 21.—Showing two tiers of prothallial cells (*pc' pc''*), primary spermatogenous cell (*p.s.c.*), and tube nucleus (*t*); ×770.

Fig. 22.—Division of primary spermatogenous cell; ×770.

Figs. 23–26.—Series of transverse sections of a pollen grain: *pc'*, basal tier of prothallial cells; *pc''*, second tier; *tn*, tube nucleus; *bcn*, body cell nucleus; *bc*, body cell; *sc*, stalk cell; *scn*, stalk cell nucleus; ×770.

Fig. 27.—Shedding stage of pollen grain; ×770.

Fig. 28.—Body cell about October 15; ×385.

Fig. 29.—A male cell just before fertilization; ×385.

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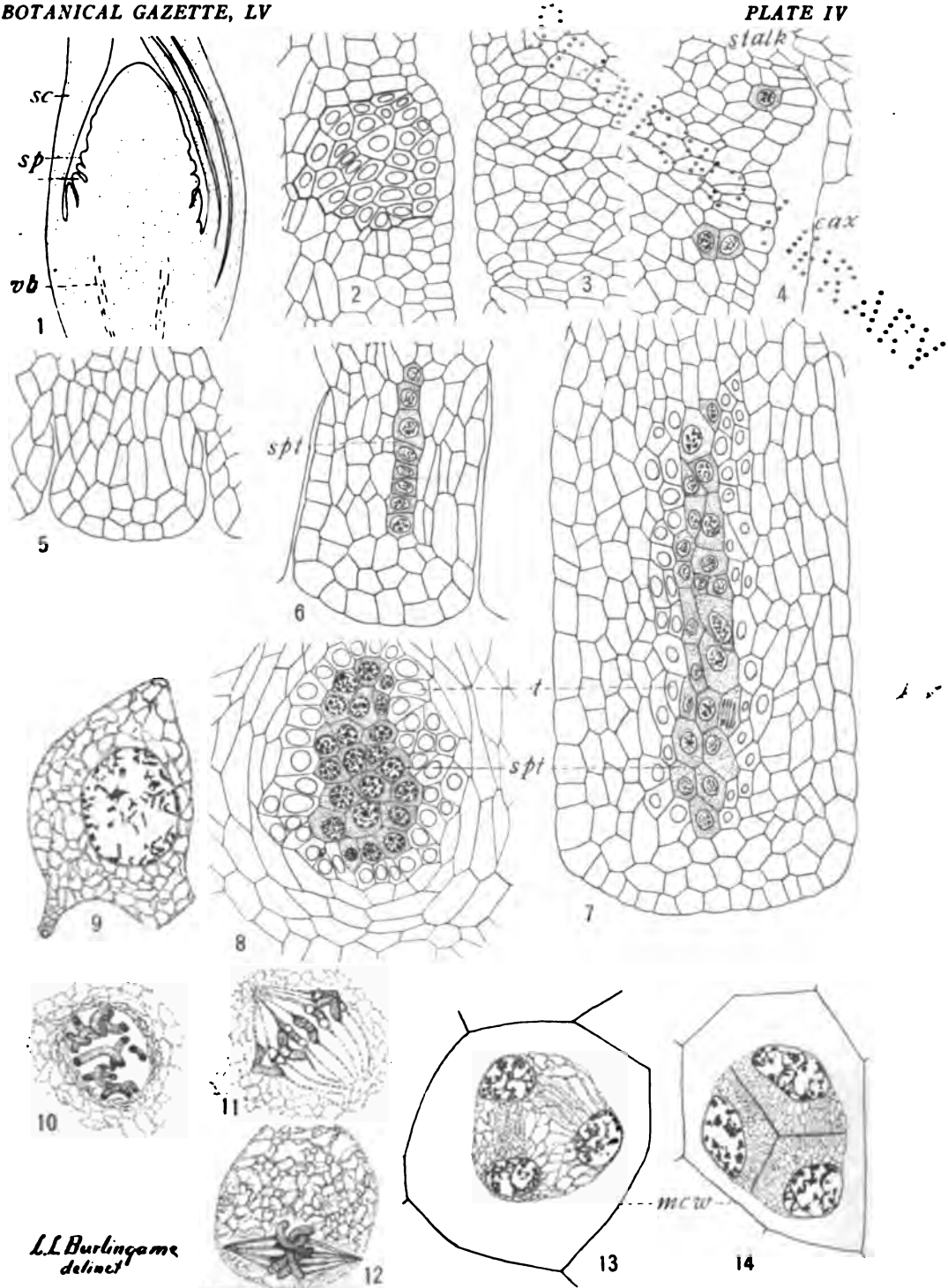

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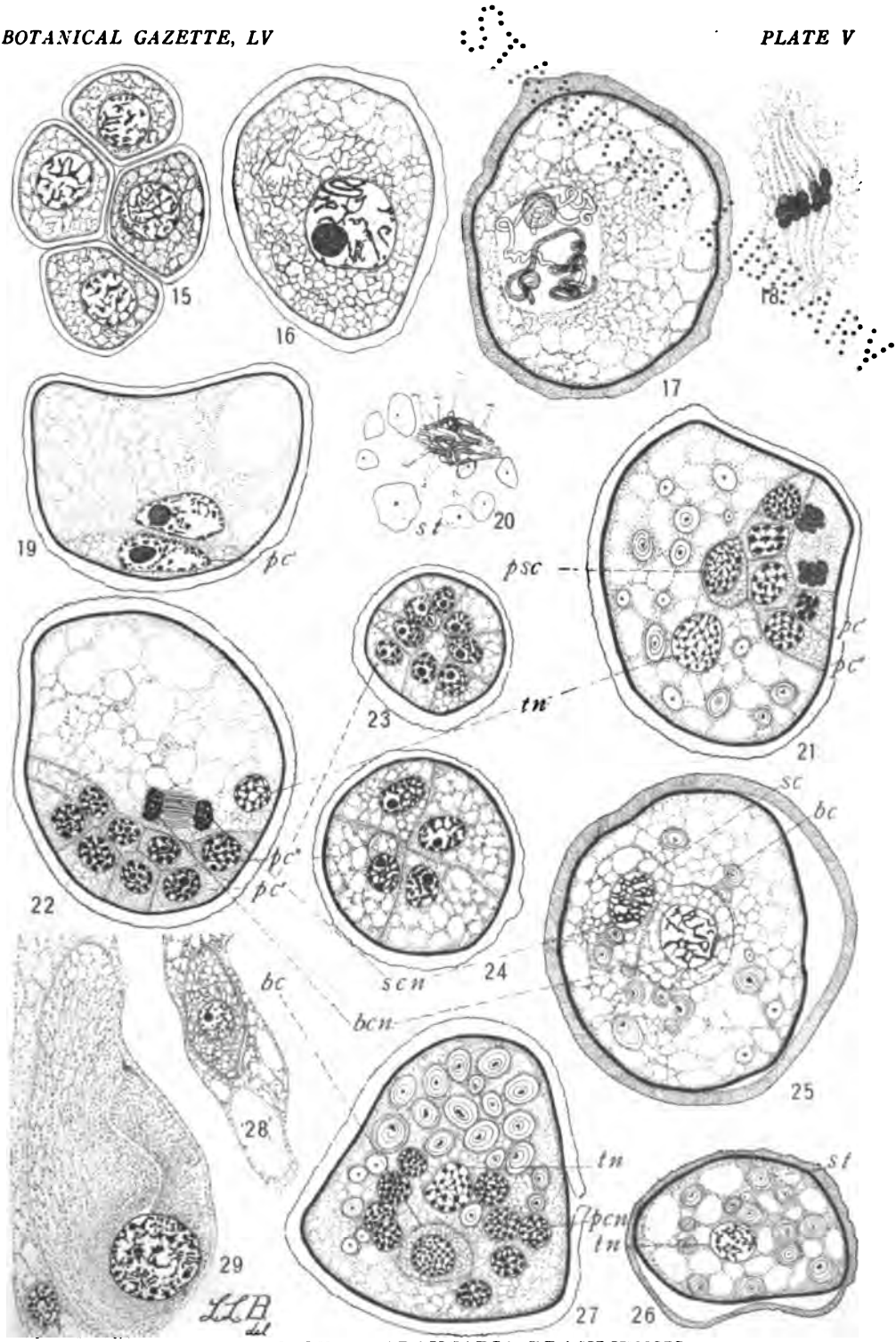

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THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. II

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH SIXTEEN FIGURES)

Part II.—The successions

THE PRIMARY SUCCESSIONS

The xerarch successions

I. Physiographic development of the habitats and description of present shores

The physiographic development of the shore habitats is in large part that of the island itself, which has been briefly outlined in the introduction. Since the postglacial history of Isle Royale has been one of gradual emergence from the waters of Lake Duluth and its successors, it follows that all parts of the island have at some stage of the process been shore.

The present shores of Isle Royale may be classified in several ways. First, there are the rock shores and the beaches, of which the former are vastly the more important. The rock shores may be classified in three ways: according to degree of slope, degree of shelter, and kind of rock involved. According to slope we find two classes: cliff shores and gently sloping shores. These two types are usually sharply distinguished. The cliffs are characteristic of the northwest coast of the island and of its surrounding islets, being produced by the broken edges of the lava and sedimentary layers; while on the southeast coast, the slope of the shores corresponds rather closely with the dip of the rocks, which is nearly everywhere gentle, averaging perhaps 10–15°. The cliffs range from 1 to 20 m. or more in height, are frequently perpendicular, and may sometimes be seen to descend without a break to considerable depths below the surface of the water. According to degree of exposure the shores, both cliff and sloping, may be divided

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into those exposed to the lake winds and waves, and those protected from them. In classifying according to kind of rock, the physical, not the chemical, characteristics are the important ones. The rocks of Isle Royale are partly volcanics, which are resistant, and subordinately sedimentaries (sandstones and conglomerates), which are much less so. On the southeast coast of the island the shores, where of volcanic rock, have smooth sloping surfaces, and where composed of sandstone or conglomerate are often much broken and

FIG. 15.—Outer shore of Long Island, southeast of Siskowit Bay: sandstone beds dipping southeast; a glacial bowlder of granite in the foreground; notable disintegration of the sedimentary rock is exhibited; the forest extends low down because the force of the waves is broken by irregularities of the shore (cf. fig. 27, where the degree of exposure is the same).

very irregular (compare figs. 24 and 15). Striking differences in rate of erosion were noted on the northwest coast. Near Blake Point the great "Greenstone" layer, which forms the backbone of Isle Royale, is at the shore, and forms smooth cliffs which rise direct from the water to a height of 20 m. or more. The stable character of these cliffs is shown by the thick coating of lichens which covers them, the belt of brilliant orange *Placodium* being especially conspicuous. Trees of large size, as well as many smaller

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plants, are abundant in the crevices (fig. 16). Very different is the shore just southwest of McCargoe's Cove (Sec. 23, T. 66 N., R. 35 W.). The material here is a sandstone, and the cliff is being rapidly eroded by the waves. Lichens are absent, and the soil and forest growth at the top are being undermined. Several recently overturned trees were seen. On the whole, wave erosion at the present lake level has not yet notably modified the configuration of the coast, so that shore recession need not be reckoned with as an important influence upon the vegetation.

FIG. 16.—Inward-facing cliff of one of the small islands bounding Rock Harbor on the southeast: resistant volcanic rock produces stable cliffs; because of sheltered location the limit of forest extension is near the water's edge, but the trees are confined to ledges and crevices.

II. The rock shore succession

With regard to the comparative areas which have been vegetated through the instrumentality of the various successions, both hydrarch and xerarch, the rock shore succession is by far the most important of all. A conservative estimate would indicate that at least nine-tenths of the forest of Isle Royale has developed along the line of this succession. At the same time it is a comparatively simple one, and will not require extended treatment.

The fundamental fact in the process, throughout the history

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of the island, has been the occupation by vegetation of new areas left exposed by the retreating waters. Recession has now ceased, temporarily at least, and no fresh surfaces have been presented for a long period of time. The forest in its advance has for this reason in some places practically reached the limit of possible growth, being prevented from further extension by wave and ice action. In these places the forest is seen extending in its full development to a line where it ends abruptly, being separated from the water by a strip of nearly bare rock shore. At other points invasion is still actively in progress, and the transition from bare shore to mature forest is a gradual one. It is in such situations as these that the various stages in the succession are seen in their best development.

On all the types of rock shore, cliff and sloping, protected and exposed, of all kinds of rock, the successional stages and processes are in general essentially the same. There are, however, important modifications due to the differences in habitat just mentioned. Among them are telescoping, suppression, or elimination of certain stages, and variations in rapidity of invasion. In the following paragraphs the complete series of stages which constitute the rock shore succession will be first described, with the understanding that rarely will this series be found in absolute entirety. Afterward the modifications of the series associated with the different types of rock shores will be discussed.

a) The complete series

In tracing the early stages of the rock shore succession we find three separate lines of advance, which may conveniently be termed *subsuccessions*. They are the rock surface subsuccession, the crevice subsuccession, and the rock pool subsuccession. Later these unite, and the development proceeds thenceforth along a single line.

1. *The rock surface subsuccession.*—We have here mainly a study in the ecology of lichens, to which adequate treatment can be given only by a specialist in that group. The general sequence of stages has been frequently described in ecological papers, as by WHITFORD (**59**) for the southern shore of Lake Superior. Crustose lichens are the first plants to appear, and are accompanied by xero-

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phytic mosses, principally *Grimmia ovata* Web. and Moore. A brilliant orange band of the lichen *Placodium* is a prominent feature of cliffs, its lower edge 2 m. above the water. This band is also distinguishable, though much less prominent, on the sloping shores. Next come foliose lichens, with the mosses *Hedwigia albicans* (Web.) Lindb. and *Orthotrichum anomalum* Hedw., and finally appear the fruticose forms, prominent among them the three large species of *Cladonia*, *C. rangiferina* (C.) Web., *C. sylvatica* (C.) Hoffm., and *C. alpestris* L.; also species of *Stereocaulon* (fig. 17).

FIG. 17.—Rock surface at Chippewa Harbor partially covered with a mat of cladonias; paucity of crevices resulting in very slow invasion; jack pines, pioneers of the xerophytic forest stage, in the background at the left.

The conditions on these bare surfaces are obviously severe, and without the aid of crevice plants vegetation advances very slowly upon them. Below they are frequently swept clean by the waves, and above, the wash of the rain keeps them clear of all débris except that of large size. Only in hollows can any gravel or humus accumulate, and only in such places does any moisture remain. As the lichen vegetation increases in bulk, soil and moisture are more and more conserved, and occasional herbs and low shrubs, and even trees, come in. Where there are few or no crevices, however, the process is so slow that such areas frequently become surrounded by mature forest, though the vegetation upon them may not have advanced as far as the heath-mat stage. Such "rock openings" are common in the forest upon the lower ridges. One of them, near Siskowit Lake (Sec. 32, T. 65 N., R. 35 W.), deserves description and illustration (fig. 18).

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This opening was about 50 m. long by half as wide, and was surrounded by the climax forest, which ended rather abruptly at its edge. The surface of the rock was very smooth, little weathered, with very few crevices. A mat composed of mosses and cladonias covered it except for scattered irregular areas which bore only a few foliose and crustose lichens. The mat had started from numerous centers, forming at first more or less circular patches which later had partially coalesced. The thickest portions were composed principally of *Cladonia rangiferina*, *C. sylvatica*, and

FIG. 18.—Rock opening in the climax forest near Siskowit Lake: cladonias (lighter patches) are dominant; masses of the moss *Rhacomitrium* (darker areas) border the *Cladonia* patches; a few small areas of bare rock; *Cryptogramme acrostichoides* and other plants growing upon the mat.

C. alpestris, and around the edges of the patches and making up the thinner portions was a growth of the moss *Rhacomitrium canescens ericoides* (Web.) Schimp. Growing upon the thicker portions were scattered plants of *Cryptogramme acrostichoides*, *Diervilla*, *Arctostaphylos*, and a few others. The whole mat could be lifted from the rock, there being absolutely no connection except where the younger plants of the moss (*Rhacomitrium*) were feebly attached. This species was evidently the pioneer, and the cladonias later had become superimposed upon it. From this area we learn that a

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luxuriant mat of vegetation may form upon a bare rock surface without the aid of crevice plants. The process, however, is exceedingly slow, and the mat thus formed is not so firmly attached and so surely permanent as that which is bound together by the trailing stems from the crevices.

2. *The crevice subsuccession.*—Crevices due to bedding planes, joints, and to differential weathering occur more or less commonly in all the rocks of Isle Royale. Where they are abundant the stages of the rock shore succession are passed through rapidly; where they are rare the process moves slowly. The soil which forms

FIG. 19.—*Potentilla tridentata* as a crevice plant; outer shore of Mott Island

in the crevices through disintegration of the rock, or is washed into them from the surrounding surfaces and the forest above, or is carried to them by the wind, is held within them, at least in part. Water flowing into or through the crevices also is retained. They form natural collecting places for seeds carried by wind, birds, and surface wash. Thus it is not surprising that nearly every crevice, large or small, is peopled by plants of many kinds. The number of species found growing as crevice plants is very great, and includes forms ordinarily occurring in diverse habitats. There are listed in my field notes 100 species, or one-fifth of the recorded flora of Isle Royale, as growing in crevices upon rock shores, and this list includes such forest plants as *Maianthemum canadense*,

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Cornus canadensis, *Clintonia borealis*, *Mitella nuda;* and such bog forms as *Andromeda glaucophylla*, *Ledum groenlandicum*, *Aspidium Thelypteris*, and *Drosera rotundifolia*. Aside from these incidental occurrences, there is a group of species that inhabit crevices on the shores everywhere and which are rarely found in other habitats. By far the most important of the early arrivals on account of its abundance and densely tufted growth is *Potentilla tridentata* Ait. (three-toothed cinquefoil) (fig. 19). Other noteworthy pioneers are *Campanula rotundifolia* L. (bluebell), *Solidago hispida* Muhl. (goldenrod), *Achillea Millefolium* L. (yarrow), *Aster ptarmicoides* T. & G., *Saxifraga tricuspidata* Rottb. (three-toothed saxifrage), *Deschampsia caespitosa* (L.) Beauv. (hair grass), *Trisetum spicatum* (L.) Richter. Another group of plants deserves mention. These inhabit moist sheltered crevices and are also characteristic of the margins of rock pools. They are *Primula mistassinica* Michx., *Pinguicula vulgaris* L. (butterwort), *Selaginella selaginoides* (L.) Link, *Lycopodium Selago* L., *Polygonum viviparum* L. (alpine buckwheat), *Tofieldia palustris* Huds. (false asphodel), *T. glutinosa* (Michx.) Pers., *Parnassia palustris* L. (grass of Parnassus), *P. parviflora* DC, *Carex atrata* L. var. *ovata* (Rudge) Boott, *C. bicolor* All., *C. Halleri* Gunn., *C. paupercula* Michx. var. *pallens* Fernald, *Allium Schoenoprasum* L. var. *sibiricum* (L.) Hartm., *Empetrum nigrum* L. (crowberry), *Euphrasia arctica* Lange (eyebright), *Prenanthes racemosa* Michx. (rattlesnake root), *Calamagrostis hyperborea* Lange. Especially characteristic of moist cliffs are the mosses *Swartzia montana* (Lamk.) Lindb., *Tortula ruralis* (L.) Ehrh., *Encalypta procera* Bruch, *E. ciliata* (Hedw.) Hoffm. The result of occupation by these classes of plants is the accumulation of humus; with the accompanying decomposition of the adjacent rock.

With these plants, or usually somewhat later, come in certain low shrubs, among them two blueberries (*Vaccinium uliginosum* L. and *V. pennsylvanicum* Lam.). More important than these, in fact most important of all the crevice plants, are the trailing shrubs, the two junipers (*Juniperus horizontalis* Moench and *J. communis* L. var. *depressa* Pursh) and the bearberry (*Arctostaphylos Uva-ursi* (L.) Spreng.). With them should be included, although it

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is ordinarily a tree, the arbor vitae (*Thuja occidentalis* L.), which frequently sprawls over the shore rocks after the manner of a prostrate vine.

Finally the trees also appear as crevice plants, and not always last in time, for young seedlings and even aged but stunted individuals are often found inhabiting the same crevice with the earliest herbaceous pioneers. Sometimes the largest cracks are lined with fair-sized trees while the rock surfaces between them are inhabited only by foliose lichens and cladonias. Any tree species may be a crevice pioneer, but *Betula alba* var. *papyrifera* occurs most frequently, with *Pyrus americana*, *Thuja occidentalis*, and *Abies balsamea* next in abundance. Growth in early years is sometimes of average rapidity, but the severe conditions soon make themselves felt, and those trees that survive increase in size very slowly. A white spruce 1 m. high and 8.75 cm. thick was found to be 87 years old, and a balsam of the same height but only 7.5 cm. thick showed an age of 123 years.

The preeminent importance of this subsuccession in the development of the forest should be emphasized. Through the soil and moisture-conserving capacity of the crevices and the resulting abundance and variety of their vegetation, and particularly because of the presence of creeping mat-forming shrubs, the establishment of the climax forest is very much hastened.

3. *The rock pool subsuccession.*—Much less important than the two preceding, but nevertheless contributing somewhat to the development of the forest by reason of the considerable amount of humus formed through its agency, is the rock pool subsuccession. Depressions of all shapes and sizes are common upon the rock shores (fig. 20). When they are of such a form as to contain standing water, the establishment of vegetation in them is quite different from that displayed in the crevices or upon the rock surfaces. Rain and waves furnish the water, which is frequently only temporarily present. The subsuccession is thus hydrarch in general but its development is subject to interruptions due to partial or entire desiccation. In the smaller depressions, which usually contain water only part of the time, vegetation when present is of the crevice type. In the larger basins which contain

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pools that are nearly or quite permanent, the development is truly hydrarch; and zonation like that found in bogs, but of a simpler type, is usual. On account of the shallowness of the water the bog mat is seldom floating. By far the most important plant in the subsuccession is *Scirpus caespitosus* L., which starting its growth at the water's edge gradually fills the pools with its dense hard stools. Frequently by growing across the high water outlet it raises the level considerably. Other species are occasionally more important in filling the pools. For instance, one depression was found to be partially filled by a mat composed of *Polytrichum*

FIG. 20.—Rock pool upon one of the islands bounding Rock Harbor on the southeast: *Scirpus caespitosus* at the right; *Andromeda* and *Alnus crispa* at the left.

commune L. and *Aulacomnium palustre* (L.) Schwaegr., bound together by the roots and rhizomes of plants growing upon it, among them *Potentilla tridentata*, *Iris versicolor*, *Vaccinium pennsylvanicum*. Another pool was being invaded by a mass of *Climacium americanum* Brid. Upon the turf mat habitually lives the interesting group of plants which has already been listed as occurring in moist crevices. Bog plants are frequent, especially *Drosera rotundifolia* L. and *Polytrichum strictum* Banks; and numerous crevice plants occur. Following, usually, the building of the turf mat come certain shrubs, the most important being *Vaccinium*

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uliginosum L. *Vaccinium pennsylvanicum*, *Andromeda glaucophylla*, and *Alnus crispa* also occur commonly. In some pools *Andromeda* is advancing directly into the water, the turf mat being absent. *Calamagrostis canadensis* (Michx.) Beauv. is usually a noteworthy companion to the shrubs.

4. *The heath mat.*—We have now traced the subsuccessions as far as they remain distinct. In the coalescence of the three the species of the crevice series are the active agents. Such plants as *Juniperus horizontalis*, *J. communis* var. *depressa*, *Arctostaphylos Uva-ursi*, and the *krummholz* form of *Thuja occidentalis* send out their trailing stems in all directions from the crevices in which they are anchored, winding through and among the cladonias of the rock surfaces and the various vegetation of the low places that were formerly pools. The continued growth of these three elements produces a firm compact mat, strongly attached in the crevices and depressions.

The history of an area may often be traced by an examination of the successive layers of the vegetation growing upon it. In one place four stages were discovered. Representing the first were scattered plants of *Potentilla tridentata* and *Deschampsia caespitosa* growing up through the mat and traceable to crevices in the rock beneath. Second in order was a thick layer of *Arctostaphylos* spreading over the rock in all directions but rooting in the crevices. The third stage was represented by *Juniperus horizontalis* growing over the *Arctostaphylos;* and the fourth by a few plants of the climax forest, among them *Aralia nudicaulis* and *Maianthemum canadense*. The order observed here is by no means universal; in fact, *Juniperus horizontalis* usually precedes *Arctostaphylos*.

The four important creeping shrubs differ greatly in their effectiveness in mat formation. In the case of *Thuja* the growth is too open and the branches reach too great an elevation above the surface to favor the accumulation of humus; and the same to a less degree is true of *Juniperus communis* var. *depressa*. *Juniperus horizontalis* by reason of its closely appressed habit is much superior. *Arctostaphylos* is probably the best of all, since its overlapping leaves almost entirely prevent the washing away of waste from beneath itself and other plants with which it grows. It is also

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very effective as a conserver of moisture. When the soil elsewhere is absolutely dry, that beneath a layer of *Arctostaphylos* is often found still to contain a high percentage of water.

Vaccinium pennsylvanicum becomes of importance soon after the establishment of the mat, and frequently dominates large areas in which the junipers and *Arctostaphylos* appear as relicts only.

It must not be understood that there is a distinct belt of heath mat along the entire front of the forest, or even that it is commonly found continuously over very large spaces. It usually occurs in patches more or less united, separated by areas of bare or incompletely covered rock, and with scattered trees, invaders from the forest, growing upon it. Telescoping of stages is very pronounced in the rock shore succession, so that in a limited area we frequently find representatives of the earliest pioneers, the climax forest, and of all stages between.

5. *The jack pine-black spruce stage and the establishment of the climax forest.*—It seems clear that the climax forest often follows immediately after the establishment of the heath mat. It seems equally certain that in many places a relatively xerophytic forest stage intervenes, in which the species are *Pinus Banksiana* Lamb. (jack pine) and *Picea mariana* (Mill) BSP (black spruce). *Populus tremuloides* Michx. (aspen) is also sometimes present. The conditions which determine the presence or absence of this stage were not discovered. In either case the establishment of the forest consists simply in a gradual increase in the number of trees inhabiting the rocky shores, the early advance being principally along the crevices.

The jack pine-black spruce forest is at the present day rather limited in extent. It was observed in its best development along the southeast coast of the island from the region of Lake Whittlesey to Lea Cove, and along the northwest shore of Rock Harbor for several miles. In other localities transitional stages passing into the climax were seen. Where conditions are most xerophytic *Pinus Banksiana* is dominant. In such places the trees grow far apart and there is much bare rock visible between them. Cladonias are the characteristic ground cover, *C. rangiferina*, *C. sylvatica*, and

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C. alpestris being about equally abundant. There is frequently considerable young growth of *Picea mariana* beneath the pines. The evidence derived from the examination of numerous localities indicates that such a type of forest will gradually become more mesophytic in character as the vegetation of the forest floor increases in amount and in water-holding capacity. Changes occur in the character as well as in the amount of the undergrowth. Mosses of the climax forest invade the areas dominated by the cladonias, growing around and over the masses of the lichens,

FIG. 21.—Ground cover in the jack pine-black spruce forest: the three cladonias of the heath mat (right), *C. rangiferina*, *C. sylvatica*, *C. alpestris*, invaded by the climax forest moss *Calliergon Schreberi* (left).

finally smothering them to death. *Calliergon Schreberi*, which among the forest mosses endures the driest conditions, is the most important of these (fig. 21). This species remains the most important element in the herbaceous vegetation throughout the intermediate forest stages, and frequently after the establishment of the climax type.

Picea mariana gradually increases, and at the same time the climax trees begin to be of importance. Here too the phenomenon of telescoping is to be seen, for we seldom find an area of jack

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pine-black spruce forest that is pure; that is, where there is not present a more or less important element representing the climax stage.

The penultimate stage in the succession is quite frequently seen. The jack pine has disappeared and the black spruces are present mainly as relicts. *Calliergon Schreberi* has come to share its position of dominance with the more mesophytic mosses *Hypnum cristacastrensis* and *Hylocomium proliferum;* and the climax trees have assumed their characteristic relations.

b) Effect of special conditions upon the rock shore succession

The shore vegetation as we see it today has not everywhere the same aspect, and the differences that appear are explained by the operation of the two following laws.

1. *The lower limit of possible forest extension is determined approximately by the upper limit of effective wave and ice work, the lake level remaining constant.*—The limit varies from the water level along the sheltered coves and harbors to a height of several meters upon the shores that face the lake. It is here far above the reach of the highest waves of the growing season, since the most severe storms take place during late fall and early winter (see ADAMS 4, p. 46). While depending in the main upon the size of the waves that break upon it, the position of the limit of forest extension is modified by the character of the shore. If it be rough or broken by ledges, neither waves nor ice will be projected so far as if the slope were smooth and unbroken, and the forest in the former case may thus establish itself lower. The effects of such differences may be seen by comparing figs. 15 and 27. If by reason of a gentle submarine slope or a submerged reef the waves break far from shore, the limit of forest extension may be greatly lowered.

2. *The extent to which the forestable territory has been occupied at the present day depends upon the rapidity of invasion, which is governed by the character of the rock, the angle of slope, and the degree of exposure to winds.*—Abundance of irregularities and crevices in the rock surface and the presence of large quantities of the products of disintegration tend to facilitate invasion, while smoothness of surface, paucity of crevices, and freedom from disintegration prod-

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ucts retard it. On a steep slope soil materials and seeds as well are washed away to a greater extent than on a gentle one. The effect of wind in opposing invasion consists in the drying out and blowing away of the small but valuable deposits of humus which accumulate upon the rocks, in the uprooting of scattered trees feebly anchored in the shallow soil, in the breaking off of those more firmly established, and in the increase of the evaporation rate.

The effects of these factors are seldom or never strictly separable, but in various combinations they result in the production of three

FIG. 22.—Three phases of rock shore vegetation; see text

phases of rock shore vegetation, differing from each other in respect to the position of the limit of forest extension and in the extent to which the forestable territory has been occupied. These are illustrated in the diagram (fig. 22). Both sides of the island represented are assumed to be equally exposed to wind and waves.

A represents an island which is effectually sheltered from the lake storms. Shores such as these are characteristic of the inner coves and harbors of Isle Royale. Upon the gentle slope at the right the climax forest in full development has reached the water's

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edge, and a fringe of *Alnus crispa* overhangs the bank (fig. 23). Upon the cliff at the left (fig. 22) the forest has also reached the lake level, but the trees are necessarily far apart, growing only where ledges or large crevices give them foothold. Wave action being at a minimum, the limit of possible forest extension is at the water's edge, and the conditions of surface, slope, and exposure to wind being favorable, all of the forestable territory has been occupied.

B represents the phase which is perhaps the commonest upon Isle Royale, and which shows to best advantage the various stages

FIG. 23.—Thoroughly sheltered shore of type *A:* forest to the water's edge; southeast side of Blake Point peninsula.

that make the complete rock shore succession. The limit of possible forest extension may be at the water's edge or at any line above it, according to the degree of exposure. Back of this limit there is a zone where occupation has been more or less incomplete, because of one or more of the retarding influences, unfavorable character of the rock, steep slope, and exposure to winds. The manner of invasion is plainly seen upon such shores. As we pass downward from the climax forest the trees become continually sparser and smaller, and the undergrowth more xerophytic. As we go farther only scattered trees are seen, closely confined to the crevices, and

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the intervening spaces are covered with heath mat or are partially bare. The outermost pioneers of the forest may or may not have reached the limit of its possible extension. Such a shore is illustrated in fig. 24.

Although as we pass outward the trees become less frequent and smaller, there is no corresponding decrease in age. The outermost individuals are often as old as any in the fully developed forest. The process of invasion in a given spot is a matter of much longer duration than a generation or two. Tree after tree lives its life in the same crevice and finally succumbs to the severity of the

FIG. 24.—Shore of type *B:* gradual invasion; island near Blake Point

conditions, each contributing toward the development of the future forest only the small remnant of humus resulting from its decay that is not blown or washed away. Through successive generations the number of individuals living at the same time slowly increases, until the assemblage of trees attains the character of true forest.

Certain of the larger rock openings upon the forested ridges, now 20 m. or more above the water, have not yet lost their resemblance to the shores, in spite of the dozens of centuries that have passed since the lake stood at their level. Such an opening (Sec.

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33, T. 67 N., R. 33 W.) is shown in fig. 25, and the extraordinary likeness to the shore illustrated in fig. 24 will at once be evident.

An especially interesting feature of this locality is the fact that just below the opening and extending to the water's edge of Tobin's Harbor is an area of climax forest of unusual beauty. The explanation of this is found in the physiographic history of the island. When the area of the present rock opening was actual shore the waves of the open lake broke upon it. As the water level subsided the ridge of Scovill Point appeared, affording full protection to the

FIG. 25.—Rock opening on the southeast slope of the Greenstone Range near Tobin's Harbor: when Scovill Point (right, in the distance) was submerged, this was a shore area exposed to the open lake; note likeness to fig. 24.

new shore area along the northwest side of Tobin's Harbor. Upon this latter, protected from both waves and wind, and receiving all the soil materials washed down from the slope above, invasion went on rapidly, resulting in the speedy establishment of the climax forest. The area higher up, exposed to the full force of the winds sweeping in from the lake across Scovill Point, still lingered in the early stages of the succession.

QUADRAT 7 (fig. 26) was located in the large rock opening described above. The likeness is so great that it may be taken also as representing shore conditions of type *B*. The surface of the

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rock was considerably disintegrated, and on areas not covered by the heath mat bore a rich lichen vegetation, the most important species, as usual in the late lichen stages, being the large cladonias. In the heath mat *Juniperus communis* var. *depressa* was dominant,

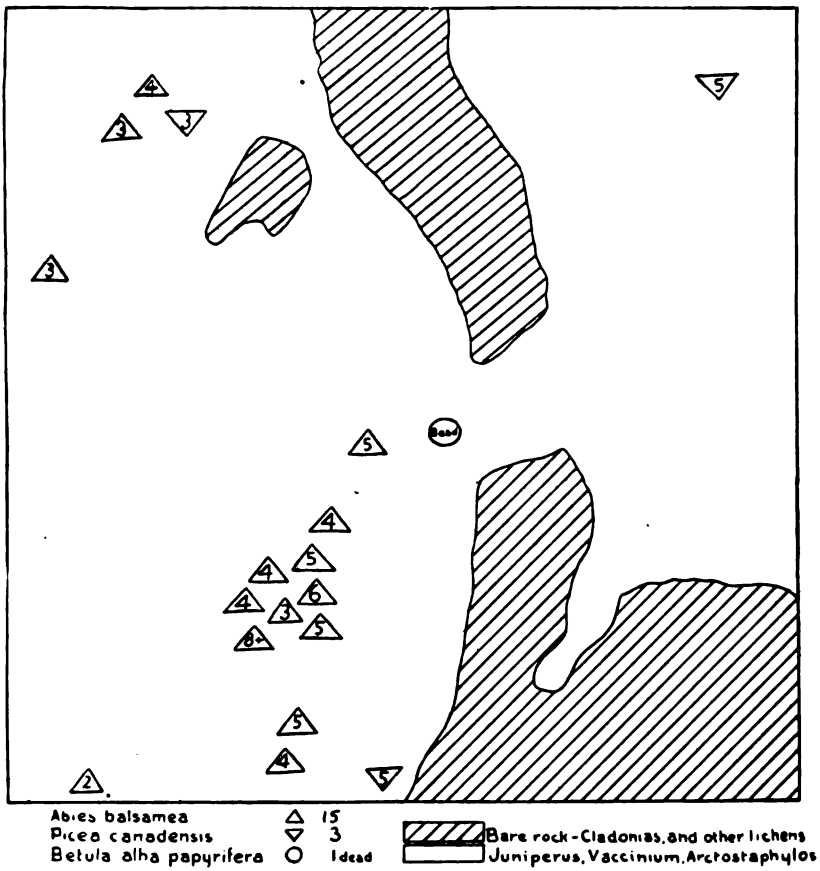

FIG. 26.—Quadrat 7: in same rock opening as fig. 25; also illustrates shore conditions of type *B*; for explanation of symbols see fig. 6.

and *Juniperus horizontalis*, *Vaccinium pennsylvanicum*, *Arctostaphylos Uva-ursi*, and *Calliergon Schreberi* shared in its composition. Crevice plants were frequent and forest herbs occurred sparingly. Undrained depressions were filled with *Aulacomnium palustre* (L.) Schwaegr. and *Scirpus atrocinctus* Fernald. These

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in earlier times may have been rock pools. Turning to the trees, we find representatives of the three climax species and no others in this particular spot. There is thus no xerophytic forest stage here, although near by scattered individuals of *Pinus Banksiana*, *Picea mariana*, *Populus tremuloides*, and *Thuja occidentalis* were noted. Balsam, the most abundant tree of the climax forest, is even here the dominant species, and this is true of the rock shores in general. None of the trees have attained great age, 50 years being the average. The rate of growth was found to vary greatly,

FIG. 27.—Shore of type *C:* limit of forest extension very high, due to exposure and smoothness of slope; note abrupt transition from bare shore to forest; one of the islands bounding Rock Harbor on the southeast.

those happily situated in regard to soil, moisture, and competition having wider rings than the less favored ones. In the rather close group below the center of the quadrat, due to a crevice, suppression was already evident, a few individuals, most of them slightly older than the others, being large and well formed, while the rest were small and stunted. Occasional standing dead trunks and frequent decayed logs remained as evidence of former generations.

C (fig. 22) represents the third type of shore, which is common along the most exposed portions of the southeast coast (fig. 27). The distinctive feature is the abruptness of the transition from

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the nearly bare rock surfaces on which the early lichens and crevice plants are almost the only vegetation, to the climax forest in its full development. Intermediate stages are often entirely lacking. The causes that bring about this abrupt transition are as follows. On account of the immediate proximity of the open lake the limit

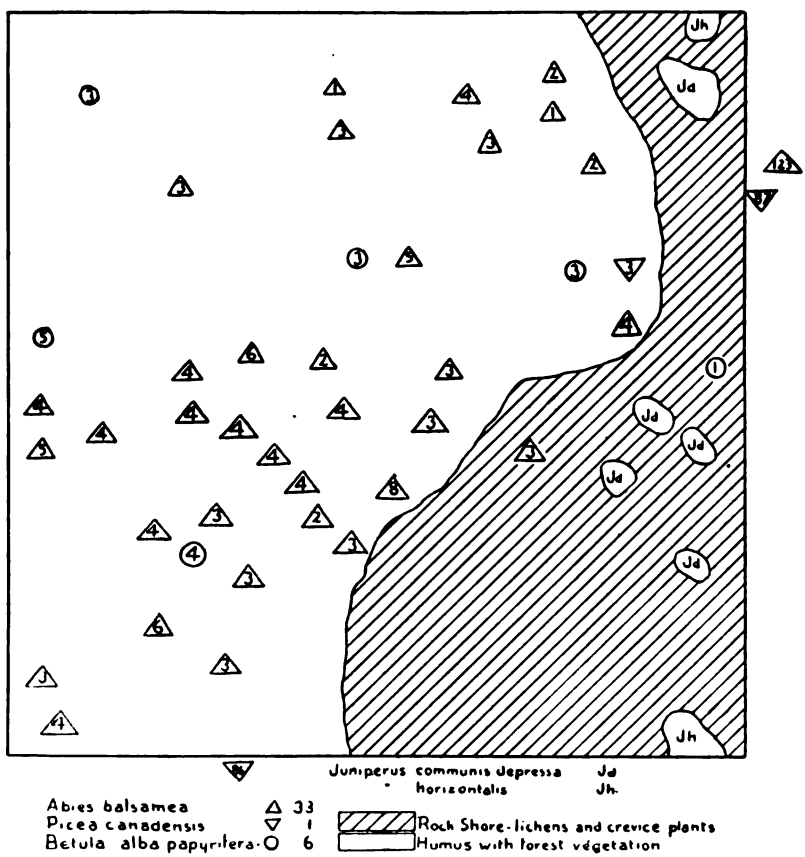

FIG. 28.—Quadrat 8: located on island illustrated in fig. 27; for explanation of symbols see fig. 6.

of possible forest extension is very high. Above this line invasion has been sufficiently rapid to bring about the development of the climax forest upon the whole of the forestable territory. The intermediate stages have been "pinched out," as it were, by the advance of the climax forest against the impregnable barrier of the waves and ice.

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A small portion of such a shore is shown in quadrat 8 (fig. 28). It was located on a small island of the outer row (Sec. 35, T. 67 N., R. 33 W.), the same that is shown in fig. 27. The line of demarcation between forest and shore is here more definite than usual, being emphasized by the presence of a slight inward-facing cliff which affords some degree of protection to the area behind it. The shore portion of the quadrat is in a rather early stage of development, the only indication of future mat formation being the patches of the two junipers shown upon the diagram, and a few scattered plants of *Arctostaphylos* and *Vaccinium pennsylvanicum* in the crevices. The forested portion might have been taken as an excellent example of the climax type. A striking feature is the zone bordering the shore area thickly peopled with young trees, mostly balsams. This is a consequence of many windfalls, resulting from excessive exposure. The spruce and balsam just outside the quadrat on the lakeward (right) side show the tenacity with which trees occasionally persist under the severest conditions, if deeply and firmly anchored in crevices. These were low scraggy individuals, very small in diameter considering their age, being respectively 8.75 and 7.5 cm. thick, and 87 and 123 years old.

c) Possible differences in the rock shore succession during the early history of Isle Royale

It must not be understood that the processes which are going on now are necessarily exactly like those that have been in operation during previous periods of the island's history. Many species, now of considerable importance, doubtless arrived upon the island long after its first emergence, and without these the balance of power may have been very different. There is no reason, however, for supposing that in their essential features the successions of the past have differed greatly from those of the present. A suggestion of what the earliest vegetation may have been, at the time when Isle Royale was merely a line of reefs barely above the surface of Lake Duluth, was obtained from a study of Gull Islands, 13 km. northeast of Blake Point. There appeared some surprising differences from the normal rock shore succession as seen upon Isle Royale itself, and the effect of the animal life upon the flora was noteworthy.

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Gull Islands.—These are a line of rocky knobs rising 1.5–12 m. above the surface of the water. They are projecting points of the Greenstone Ridge which disappears under the water at the northeast end of Isle Royale, reappears in Passage Island, and again here.

They are steep-sided in the main, and at one point on the northwest side of the largest islet there is a small shingle beach. As the name indicates, the islands are favorite haunts of the herring gulls, which congregate and breed here in enormous numbers. They are accompanied by many smaller birds and by untold millions of flies and gnats, evidently living upon the decaying animal matter, which is abundant and offensive.

The vegetation was found to be a strange mixture of shore and forest plants, the latter in spite of the bareness of the islands including some that habitually grow in deep shade. There were also other species which belonged to neither category. Wherever conditions favored accumulation, humus was deep and seemed to be composed largely of the remains of *Calamagrostis canadensis*, the most abundant species upon the islands. In some places this grass formed a thick rank growth, flowering abundantly. Over large areas there was merely a short turf, and in many places the humus was entirely bare, doubtless kept so by the gulls in their domestic operations. With *Calamagrostis* and forming a thicket-like growth was found *Pyrus americana*, and this was the only tree upon the islands. It was most abundant upon the upper part of the beach mentioned above, where a few specimens were noted that were 4 m. high and 1.5 dm. in diameter (fig. 29). There were more dead specimens than live ones, and the living showed the effects of the hard conditions in yellow and curled foliage and dead branches. Fruit was borne abundantly. Other shrubs that formed a part of the thicket were *Salix phylicifolia* L.; *Cornus stolonifera* Michx. (red osier dogwood); *Ribes prostratum* L'Her (fetid currant), fruiting in wonderful abundance; *R. oxyacanthoides* L. (prickly gooseberry); *Rosa acicularis* Lindl. var. *Bourgeauiana* Crépin; *Rubus idaeus* L. var. *aculeatissimus* (C. A. Mey.) Regel & Tiling (red raspberry), abundant; *Sambucus racemosa* L. (red-berried elder); *Taxus canadensis* Marsh (ground hemlock), frequent, forming a low matted yellowish growth partially protected

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by other shrubs; most surprising of all, *Fatsia horrida* (Sm.) B. & H. (devil's club), about six specimens with curled and yellow leaves, but all flowering.

In all, 26 species were listed, and of these only 5 are characteristic shore plants; 10 were species found ordinarily in the climax forest, but growing here with more or less success in spite of the severe conditions. The way in which many of the plants reached the island is suggested by the fact that 10 out of the 26 bear more or less edible berries. Birds have evidently been important agents in determining the composition of the flora of Gull Islands.

FIG. 29.—One of the Gull Islands: a small shingle beach with stunted mountain ash; with this grew a few plants of devil's club (*Fatsia*).

Such a type of vegetation as exists today upon these rocks may well have been the first to occupy the summits of the Isle Royale ridges when they first emerged from Lake Duluth. As the area of the island increased, and more and more species became established upon it by various means, the vegetation of the shores and the successional processes concerned therein became gradually like those of today.

III. The beach succession

a) Extent, situations, and materials of the beaches.—Beaches are numerous but not extensive upon Isle Royale. There are many

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miles of rocky coast absolutely unbroken by beaches of any kind. Wave erosion at the present lake level has not yet produced an irregular coast line, in the reentrants of which they might develop, nor has it furnished abundance of sand, gravel, and shingle for their building. The general steepness of the shores is another unfavorable feature. Such as are present occur in the bays and coves, most of which are due not to wave erosion but to the original configuration of the rocks. The fragments eroded from the bold cliffs and headlands near by are swept into these reentrants and come to rest there in the comparatively quiet water. Most of the beaches are of limited extent, but at the head of Siskowit Bay there are two magnificent stretches, separated by Senter Point, which have a total length of 2 km. The materials range from fine sand to coarse shingle, the larger sizes being by far the commoner. Back from many of the present beaches extend similar accumulations which were made when the water level stood higher than now, and formations identical in character occur at various levels upon the ridges.

b) *Vegetation.*—From their nature, beaches occupy situations that are more or less protected from the full force of waves and ice, and usually from wind also by reason of neighboring headlands. As compared with the rock shores they thus provide favorable opportunity for invasion by plants. The limit of possible forest extension, as in the case of the rock shores, varies with the effective reach of waves and ice, but is never high. Below this limit the materials are frequently moved about by the waves, and all vegetation except annuals is manifestly impossible. Even lichens must be destroyed by the movement and friction. Above the limit of the waves, where the fragments are not disturbed, conditions are particularly favorable for invasion. If the material is fine a soil is already present, if coarse there is opportunity for the accumulation of soil in the interstices of the shingle. In the latter case water drains off too rapidly, but as the openings become filled, this fault is gradually corrected.

Because of the favorable conditions enumerated above, the climax forest in most cases has already advanced to its limit of possible extension. Very often a bank of solid humus, formed

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during long ages of forest growth, marks the upper boundary of the beach. The transitional stages have thus been pinched out, and opportunities for their investigation are therefore scanty.

Where the forest ends most abruptly a line of *Alnus crispa* commonly fringes it (fig. 30). Where the transition is slightly more gradual there are suggestions of intermediate stages. Out among the shingle are found scattered herbs: *Equisetum arvense* L. (horsetail), *Epilobium angustifolium* L. (fireweed), *Deschampsia caespitosa* (L.) Beauv. (hair grass). *Rubus triflorus* Richards (dwarf raspberry) often trails over the stones for many decimeters. A more important group is made up of low shrubs, among which *Rubus idaeus* var. *aculeatissimus* (red raspberry), *Diervilla Lonicera* Mill (bush honeysuckle), *Rosa acicularis* Lindl., *Physocarpus opulifolius* (L.) Maxim. (ninebark), and *Rubus parviflorus* Nutt. (white-flowered raspberry) are most prominent. Behind these come the tall shrubs, *Alnus crispa* most important, and also *Cornus stolonifera* and several species of *Salix*. No instance of actual transition into the climax forest was observed, but it probably follows immediately after the tall shrubs.

FIG. 30.—Upper limit of shingle beach on the northwest side of the Blake Point peninsula: note large size of material; *Alnus crispa* fringing the forest.

PALO ALTO, CALIFORNIA

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MACROZAMIA MOOREI, A CONNECTING LINK BETWEEN LIVING AND FOSSIL CYCADS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 168

CHARLES J. CHAMBERLAIN

(WITH TWELVE FIGURES)

The greatest cycad centers of the world are the states of Vera Cruz and Oaxaca in Mexico and Queensland in Australia, Queensland having three genera, *Cycas*, *Macrozamia*, and *Bowenia*, and the Mexican region three genera, *Dioon*, *Ceratozamia*, and *Zamia*. As yet no other region has claimed more than two genera. In the cycad region of Australia *Macrozamia* is the dominant genus, and its various species range from the northern part of Queensland to the southern limit of cycads in New South Wales. In a more extended publication the genus and the interrelationship of its species will be discussed, but at present we shall consider only a single species, *Macrozamia Moorei*, which presents features of unusual interest. The field study was made at Springsure, about 200 miles west of Rockhampton and almost on the Tropic of Capricorn.

Macrozamia Moorei has a massive cylindrical trunk with a splendid crown of leaves (fig. 1). Most of the plants grow in the blazing sun, but some are found in the scanty shade of small *Eucalyptus* and other trees. The altitude of Springsure is about 325 m., but some plants were noticed a few miles east of Springsure, perhaps 30 m. lower, and specimens could be seen on the tops of the neighboring mountains, perhaps 300 m. higher.

The trunk is 2–3 m. high in most of the large plants; a few reached 5 m. in height, and one specimen, growing in the shade, measured 7 m. from the ground to the bud. The diameter of the trunk of this specimen was 66 cm., but there is little increase in diameter after a plant reaches a meter in height, for such plants may be 0.5 m. in diameter, and some plants 3 m. in height, and growing in the sun, measured 71 cm. in diameter.

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The foliage display is not surpassed by any cycad. The leaves are 2–3 m. in length and may number more than 100 in a single crown. With so many large leaves in a crown, and, in all probability, a new crown nearly every year, the trunk grows rapidly. Mr. J. W. KEIT, of Durban, South Africa, showed me an ovulate plant raised from a seed planted 30 years before, which had a stem reaching 25 cm. above the surface and bearing a fine crown of leaves and two large cones. Another plant, also raised from a seed

FIG. 1.—*M. Moorei* at Springsure: ovulate plant in foreground has trunk about 3.5 m. in height.

planted a few years before the one just mentioned, had a stem 40 cm. in height and had borne ovulate cones for several years. This shows that the plant grows very rapidly and produces cones at an early age. Although it is very probable that small cycads, like *Zamia*, produce cones at a still earlier age, this is the first instance, so far as I know, in which the period between the planting of the seed and the production of cones is known, even approximately.

The armor of leaf bases persists even at the base of the stem, so that the age of a plant could be estimated quite easily, if it were

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known how often new crowns are produced. If crowns are produced every year, a plant a meter in height might be considerably less than 100 years old.

Although the trunk is so massive, a transverse section shows the large pith, scanty wood, and large cortex, so characteristic of cycad stems, there being no extensive development of wood like that found in large stems of *Dioon spinulosum*. A plant about 3 m.

FIG. 2.—*M. Moorei:* transverse section of stem 45 cm. in diameter

in height, with a stem 45 cm. in diameter, had a zone of xylem and phloem only 5 cm. in width (fig. 2). In the photograph three distinct regions are shown; the innermost is the xylem, the middle one its accompanying phloem, and the outermost a second cylinder with its xylem and phloem which show clearly in the material but which are not differentiated in the photograph. The trunk, therefore, is polyxylic. The outer cylinder evidently originates in the cortex, as in *Cycas*, but is separated from the primary cylinder by only a scanty amount of parenchyma. There are

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scattered bundles in the pith, but there are no cone domes, and the scattered bundles seem to have no connection with cones. In regard to the bundles in the pith, this stem is somewhat like that of *Macrozamia Fraseri*, as described by WORSDELL.[1]

The tracheids of the xylem show two, three, or four rows of crowded bordered pits. There are uniseriate rays, similar rays two or three cells wide, and large rays containing vascular strands,

FIG. 3.—*M. Moorei:* ovulate cones about 76 cm. in length

as in *Dioon*. There is no more difference between the general and histological structure of the stems of *Macrozamia* and *Cycadeoidea* than may be found between different genera of Cycadales. Bennettitales and Cycadales could hardly be separated on the basis of stem structure.

The ovulate cones are large and are seldom borne singly, two, three, or four being more common than a single cone, and in one case

[1] WORSDELL, W. C., Anatomy of the stem of *Macrozamia* compared with that of other genera of Cycadaceae. Ann. Botany 10: 601–620. *pls. 27–28.* 1896.

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I saw eight large cones on a single plant (fig. 3). When I visited Springsure, late in November, the cones were not mature, but some of them were already 80 cm. in length and weighed 15 kilos. Dr. F. M. BAILEY, in his *Flora of Queensland*, reports cones 90 cm. in length. Scarcely any of the cones were vertical, nearly all leaning and some of them almost horizontal (fig. 1). The numerous strong leaves prevent the cone from hanging down, as it does in *Dioon spinulosum*.

FIG. 4.—*M. Moorei* with more than 50 staminate cones

By far the most striking feature of *Macrozamia Moorei* is its staminate cones and associated structures (fig. 4). Plants with 20–40 staminate cones were not at all rare, and in one case I counted 103 cones on a single unbranched plant. Not only is the number larger than has ever been reported for any cycad, but the cones are obviously lateral, as may be seen by a glance at the figure, which shows a girdle of cones outside the new crown and scattered among the leaves of the previous crown. Young cones of the next season are found among the bases of the leaves of the new crown, but there are no cones in the center of the crown.

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A tangential section through the armor at the top of the stem (fig. 5) shows a condition exactly like that seen in WIELAND's figures of *Cycadeoidea*. The peduncles of the cones, with their accompanying scale leaves, are wedged in among the leaf bases, and sections show that the cones arise in the axils of the leaves. Of course, the terminal peduncles of *Dioon* and similar forms finally become wedged in among the leaf bases, but the condition is secondary and is due to the sympodial nature of the stem; in

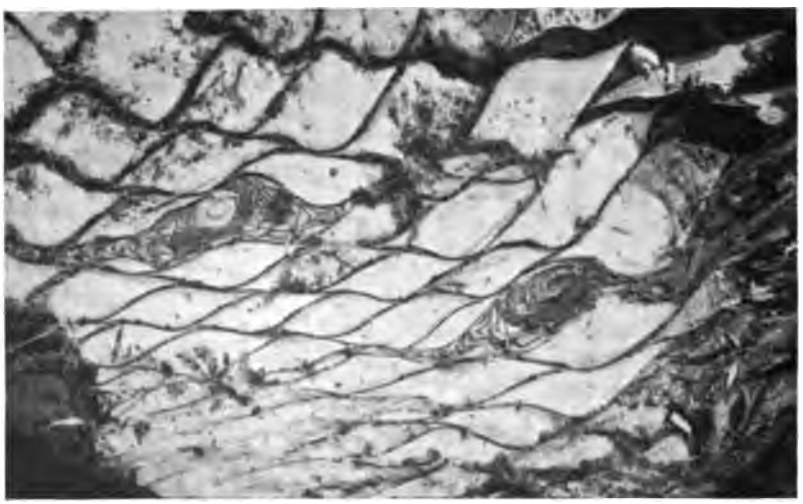

FIG. 5.—*M. Moorei:* tangential section (cut with an ax) through the armor of leaf bases, showing the peduncles of cones surrounded by scale leaves.

Macrozamia Moorei the condition is primary, the stem being monopodial, with all its cones lateral.

In all the occidental cycads, *Dioon*, *Ceratozamia*, *Microcycas*, and *Zamia*, a single ovulate cone is a rule to which there are scarcely ever any exceptions, except in *Zamia;* in staminate plants exceptions are almost as rare, except in *Zamia*, which very frequently has more than one cone, and sometimes as many as six or seven. In *Dioon*, *Ceratozamia*, and *Zamia*, in both ovulate and staminate plants, the cone domes in the pith indicate the sympodial nature of the stem. *Microcycas* has not been examined, but will doubtless show cone domes.

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Among the oriental cycads (*Cycas*, *Macrozamia*, *Bowenia*, *Encephalartos*, and *Stangeria*) the situation is not so uniform. In *Cycas* the ovulate plant does not bear a compact cone, the sporophylls having the position of a crown of vegetative leaves with the growing point at the center, the growing point persisting from the seedling throughout the life of the plant. In the staminate plant there is hardly ever more than one cone, and this is terminal. There are cone domes in the pith.

In *Bowenia*, both ovulate and staminate cones are borne singly on slender branches of the main stem.

In *Stangeria*, both ovulate and staminate cones are terminal and are usually borne singly, although occasionally there may be two or three, especially in case of staminate plants. There are well marked cone domes in the pith.

In *Encephalartos*, both male and female plants often bear more than one cone, and in some species a single cone is the exception, while three, four, and five are common. PEARSON noted that in *Encephalartos Frederici Gulielmi* the cones are arranged in a circle about the bud. In this species, at Queenstown, South Africa, where PEARSON made his observation, I saw seven ovulate cones in a circle about a well developed bud. In *E. caffer*, *E. Altensteinii*, *E. horridus*, and *E. villosus* I found three to five cones in a circle about a well developed bud. Such cones are lateral with respect to the growing point, which does not become transformed into a cone, but continues the growth of the plant. A dissection of adult specimens of *E. Altensteinii* and *E. villosus* showed no cone domes in the pith, and cone domes are necessarily present when cones are terminal. It may be doubtful whether cones are terminal in *Encephalartos*, even when produced singly.

In various species of *Macrozamia* ovulate plants frequently bear more than one cone, and in staminate plants more than one cone is the rule. Both ovulate and staminate cones are obviously lateral, even when borne singly. There are no cone domes in the pith.

Of course, in all the genera, when there is branching in the popular sense of the term, each branch may bear a cone.

Since *Macrozamia Moorei* approaches so closely to the Ben-

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nettitales, it is worth while to consider how a compact cone has probably been derived from a loose crown of sporophylls, and how the terminal position of cones may have succeeded the lateral. The compact cone, found everywhere in living cycads, except in the ovulate plant of *Cycas*, has in all probability been derived from a loose crown of sporophylls like those of the Cycadofilicales and the staminate sporophylls of Bennettitales, and like the ovulate sporophylls of *Cycas*. Various species of *Cycas* show stages in the advance from this loose crown of leaflike sporophylls toward the compact cone composed of sporophylls so highly modified that their leafy nature is very much obscured. In *Cycas revoluta* the sporophylls are quite leaflike and bear five or more ovules; in *C. circinalis* the pinnae are much more reduced, appearing only as serrations on the edge of the much reduced blade; in *C. media* the sporophyll is equally reduced and frequently bears only two ovules; in *C. Normanbyana* the sporophyll is about as in *C. media*, but there are regularly only two ovules. From the sporophyll of *C. Normanbyana* to that of *Dioon edule* the transition is easy, and the loose cone of *D. edule* does not differ much in appearance from early stages in the development of the ovulate structures of *Cycas*. The distinguishing feature is that in the ovulate plant of *Cycas* the meristem never becomes converted into sporophylls, but continues the growth of the axis. From the condition in *Dioon* to the more compact cones of the remaining genera, the transition is easier still, and consists principally in shortening the blade of the leaf until it finally reaches the almost peltate sporophyll of *Microcycas* and *Zamia*. Occasionally a proliferating cone reminds one of the *Cycas* condition.

In the reduction of the number of cones, and in the evolution of the compact cone from a loose crown of sporophylls, we have two independent series of changes, which may or may not have progressed with equal rapidity. Loose staminate sporophylls and numerous lateral cones are characteristic of the Bennettitales. The combination of loose sporophylls and numerous lateral cones is not found in any living cycad, but loose sporophylls are found in the ovulate plant of *Cycas*, and numerous lateral cones are found in *Macrozamia Moorei*, the staminate cones being almost as numerous

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as in Bennettitales; while in other species of *Macrozamia* and in *Encephalartos* the lateral cones are present but not so numerous. In a reduction from numerous lateral cones to a single cone, the natural limit would be the single terminal cone developed from the apical meristem, and with the transformation of the apical meristem into a cone, the formation of a cone dome in the pith would be a necessary consequence. Accordingly, the absence of cone domes from *Macrozamia* and *Encephalartos* is easily understood.

Macrozamia Moorei, in its numerous lateral cones and in their mode of occurrence, presents a condition identical with that found in *Cycadeoidea* among the Bennettitales. As far as the mode of bearing cones is concerned, *Macrozamia Moorei* makes the transition from Bennettitales, like *Cycadeoidea*, to the modern cycads an easy one. In the structure of the individual cone, the transition is not so easy, but may become less difficult when more is known about the cones of the Bennettitales, especially the lower Bennettitales. The connection between the higher Bennettitales and the Cycadales, already a close one, is made still closer by *M. Moorei*, so that it might be doubted whether the differences are great enough to distinguish orders.

The male gametophyte

The pollen grain at the time of shedding contains three cells, a persistent prothallial cell, a generative cell, and a tube cell (fig. 6). As pollen shaken out from the cone loses a little moisture, it begins to collapse so that in a vertical view the grains appear elliptical, with a long narrow area at the top which does not stain when safranin is added (fig. 7). This elongated area becomes narrower as the grain dries and finally the sides come into contact. A study of sections shows that this elongated area at the top of the grain is not covered by the exine, but only by the intine, a situation which is constant in *Ginkgo*, but which has not been noted in cycads. Just beneath the portion not covered by exine there is usually a funnel-shaped depression. The cytoplasm of the pollen grain is quite dense and contains starch.

The pollen from which figs. 6 and 7 were drawn was shaken from a cone in the Botanic Gardens at Sydney on November 3, 1911,

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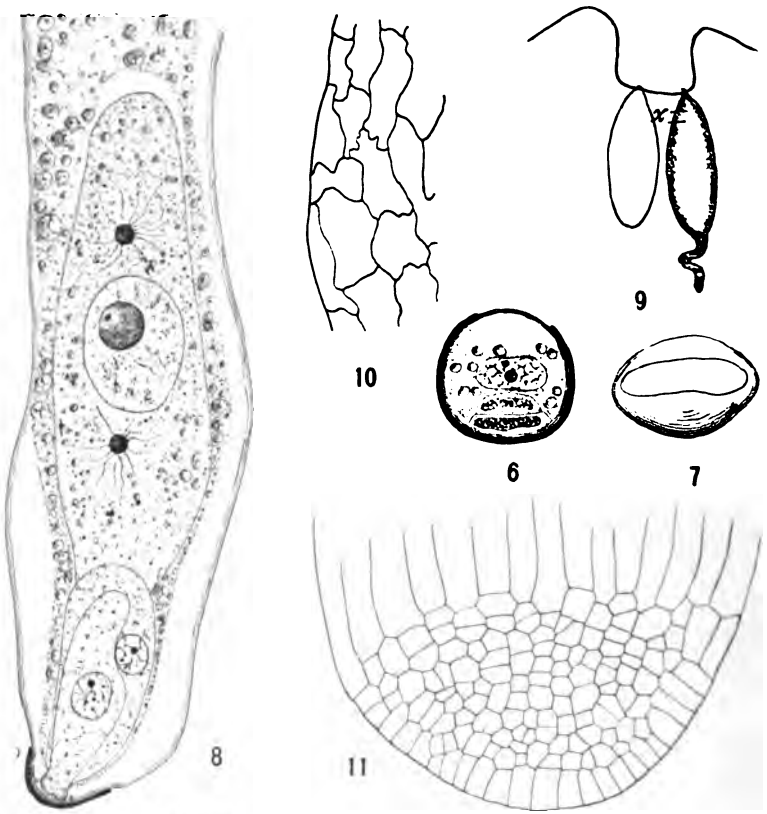
and the condition of the staminate cones in the field at Springsure, about 1100 miles farther north, on December 1 would indicate that in the field the pollen had been shed at about the same time, or perhaps a little earlier. On December 1 the generative cell has



FIGS. 6–11.—*M. Moorei:* fig. 6, pollen grain at the shedding stage, November 3, 1911, showing prothallial cell, generative cell, tube cell, and starch grains; ×800; fig. 7, pollen grain; the elongated area is not covered by exine; ×800; fig. 8, pollen tube, December 1, 1911; ×480; fig. 9, upper part of female gametophyte, February 1912, showing deep archegonial chamber and young embryo; ×6; fig. 10, portion of parietal tissue of proembryo at *x* of fig. 9; ×130; fig. 11, tip of embryo shown in fig. 9; ×58.

already divided, forming the stalk and body cells, and the blepharoplasts have appeared (fig. 8). The pollen tube structures at this stage are about as in *Dioon*, there being scarcely any branching of

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the tube and none of the peculiar basal haustoria which characterize the pollen tubes of *Ceratozamia*.

The condition of the male gametophyte when the pollen is shed is remarkably uniform in the family, no exception to the three-celled stage having as yet been demonstrated. IKENO found this condition in *Cycas revoluta*, and Miss FRANCES G. SMITH found it in *Encephalartos villosus*. I have observed it in *Dioon edule*, *Ceratozamia mexicana*, *Microcycas calocoma*, *Zamia floridana*, *Bowenia spectabilis*, *Macrozamia Miquelii*, *M. spiralis*, and *Stangeria paradoxa*; so that it occurs in all the genera. The behavior of the three cells is also similar, the prothallial cell pushing up into the stalk cell in all the genera, with the possible exception of *Cycas*.

Since the structure of the pollen grain is so uniform in the cycads, it would be interesting to know just what the structure is in fossil Cycadales and Bennettitales. A more extensive development of prothallial tissue and a comparatively slight development of the pollen tube or haustoria might be anticipated.

The female gametophyte

Early in November, when the ovulate cones have attained a length of 78 cm., the female gametophyte has reached its full size, but by no means its full density. The archegonia, generally 4–6 in number, are a little more than 3 mm. in length and are becoming filled with protoplasm and foodstuffs. The ventral canal nucleus has not yet been cut off and the archegonial chamber has just begun to develop. At the fertilization stage, most of the cells of the female gametophyte contain large starch grains; the rest contain tannin. The archegonial chamber is the deepest ever noted in a cycad, the average depth being about 1.8 mm., so that the depth is nearly two-thirds as great as the length of the archegonium (fig. 9).

The embryo

The earlier stages in the development of the embryo are not available, but arrangements have been made to secure them. The earliest stage in our material is shown in fig. 9. At this stage *Macrozamia Moorei* differs from *Dioon edule*, *Ceratozamia mexicana*, and *Zamia floridana*, but agrees with *Cycas revoluta* and perhaps

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with *C. circinalis*. In *Zamia* and *Ceratozamia* fertilization is followed by a series of free nuclear divisions and finally cell formation takes place only at the bottom of the egg, less than one-fifth of the egg becoming segmented, while the rest remains in the free nuclear condition. In *Dioon edule* the free nuclear stage is followed by an evanescent segmentation of the entire egg, but later

FIG. 12.—*M. Moorei:* a poisoned plant

stages show segmentation only at the bottom of the egg, with free nuclei above. *Macrozamia Moorei*, in the only stages available, shows complete segmentation, but a large vacuole has already developed, and within the limits of the egg there remains only a cellular layer two or three cells in thickness (fig. 10). Material of *Cycas revoluta* in this stage, furnished me by IKENO several years ago, shows exactly this condition. Whether both have passed through a stage of complete segmentation, as in *Ginkgo*, or segmentation

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has occurred only at the periphery, the vacuole having been formed by the breaking down of free nuclear material, are questions which could be answered by a glance at material in the desired stages. The extensively segmented proembryos of *Macrozamia* and *Cycas*, and even the temporarily segmented proembryo of *Dioon*, are, in our opinion, more primitive than the proembryos of *Zamia* and *Ceratozamia*, which are segmented only at the base.

At the stage shown diagrammatically in fig. 9 and quite accurately in fig. 11, the differentiation into suspensor and embryo proper is quite distinct, but there is not yet any differentiation of plerome and periblem or even dermatogen; the outer layer of large absorbing cells still showing numerous periclinal divisions.

Unfortunately, the young leaves of *Macrozamia* contain a poison which causes a kind of paralysis in cattle, and consequently the plant is in bad repute among cattlemen. At Springsure, the only habitat mentioned for *M. Moorei*, the plant is being exterminated so rapidly that in a few years it may be hard to find a specimen. In killing the plant, a notch is chopped in the trunk and a large hole is then bored from the notch to the center of the pith (fig. 12). The hole is filled with arsenic and the plant soon dies. The dead specimens become quite brittle and are soon broken down by the wind. The notch and the characteristic appearance of a poisoned specimen are shown in fig. 12. The species is beautiful and grows rapidly, but it is almost never found in botanical gardens and conservatories. It would be a pity to allow a plant with such good claims to the title of missing link to become extinct, in spite of the fact that it is easily accessible.

Summary

1. *Macrozamia Moorei* bears numerous lateral cones in the axils of leaves, in this respect being identical with the mesozoic Bennettitales.

2. The pollen grain, at the time of shedding, contains a persistent prothallial cell, a generative cell, and a tube cell; the exine does not cover the apical part of the grain. In the young pollen tube the generative cell has given rise to a stalk cell and a body cell like those of other cycads.

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3. The archegonial chamber is unusually deep, and the archegonia are of moderate size.

4. The embryogeny resembles that of *Cycas* and differs from that of *Zamia* and *Ceratozamia*.

5. The species, which represents the nearest approach to the mesozoic Bennettitales, is in immediate danger of extinction.

UNIVERSITY OF CHICAGO

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A PROTOCORM OF OPHIOGLOSSUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 167

LOREN C. PETRY

(WITH THIRTEEN FIGURES)

Historical

The earliest description of the growing region of *Ophioglossum vulgatum* is by BRAUN (4) in 1839. He recognized the spiral arrangement of the leaves and described the sheathing of the growing point. HOFMEISTER (9) in 1857 described the apical cell of the same species as triangular in transverse section; its exact form was not stated. The vascular cylinder was described as a loose network with a large gap corresponding to each leaf. However, he stated that the bundle connecting with the leaf is sent off from the upper angle of the gap. RUSSOW (13) gave the histological details of the structures of *O. vulgatum*, and pointed out the positions of protoxylem and protophloem.

The first extensive description of the anatomy of this species is by HOLLE (10). He refuted HOFMEISTER's statement that the leaf trace attaches to the upper angle of the gap. He further stated that there is a root corresponding to each leaf and that the bundle of the leaf trace is continuous with that of the root inserted immediately below it. The apical cell is described and figured.

VAN TIEGHEM (14) in 1890 discussed the transition of the vascular cylinder of *O. vulgatum* from a solid stele to the medullated condition, and described an endodermis surrounding each bundle of the mature stem. ROSTOWZEW (12) described the development of young plants of this species from buds upon roots. His figures indicate that the apical cell is sometimes a truncated pyramid.

BOWER (1) in 1896 described the vascular anatomy of *O. Bergianum* as resembling closely that of *O. vulgatum*. He discussed the anatomy of the latter species and decided that the relation between root and leaf is variable. BRUCHMANN (5) described the development of the embryo of this species. The vascular develop-

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ment of the sporeling is not given, but it is stated that it follows that of the bud as described by ROSTOWZEW (12).

BOWER (2) in 1904 described the vascular structures of *O. simplex* and *O. pendulum*. In the latter species the many strands of the petiole unite to form 5 bundles which unite separately with the vascular cylinder. CAMPBELL (6) described the usual form of the apical cell of *O. pendulum* as a triangular pyramid; a truncated triangular pryamid was found occasionally. The first division of the segment of the apical cell is transverse. The same author (7, 8) later described the development of the embryo of *O. moluccanum*. The embryo consists of cotyledon and root only; no stem is recognized. The leafy plant arises from a bud upon the root of the embryo.

BOWER (3) in 1911 described the vascular structures of *O. palmatum*, which constitutes the division CHEIROGLOSSA. The stele is a very loose network. The leaf trace is double and the two strands connect with the vascular cylinder at opposite sides of the common gap. Roots are diarch or triarch and sometimes occur within the pith. BOWER concluded that the double leaf trace is a derived condition.

LAND (11) described very briefly a protocorm found in material of *O. vulgatum* from southern Mexico. No details of the structure were given.

Investigation

The protocorm described by LAND (11) is the subject of this investigation. Its size and general appearance are described in that paper. The specimen was sectioned and examined with especial reference to its vascular anatomy and apical region.

As already stated, the protocorm is approximately spherical and about 9 mm. in diameter. The growing point is at the bottom of a circular pit which extends downward about 0.8 of the diameter of the corm (fig. 1). The functioning leaf arises from this pit and its base is attached to the side of the pit at a distance of about 2 mm. above the growing point. Above the base of the functioning leaf the bases of 6 other leaves are present, and below it the primordia of 6 others occur. The leaves are arranged in an

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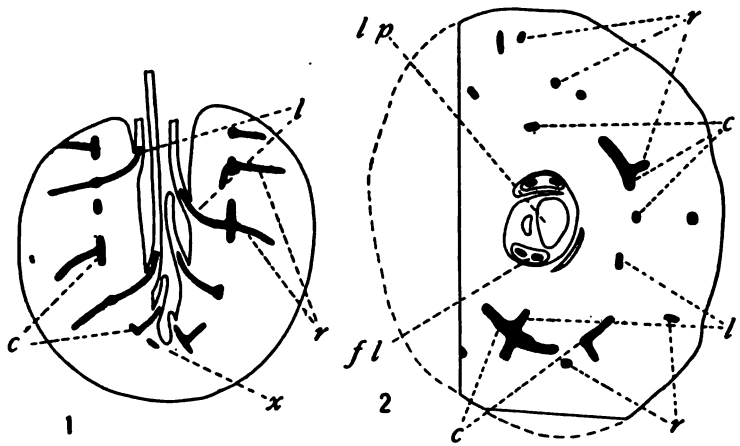
irregular spiral approximating the $\frac{2}{5}$ arrangement that has been described for this species.

The vascular tissue all occurs *above* the growing point, that is, surrounding the circular pit from which the leaves arise (figs. 1, 2). Each leaf trace consists of two strands which connect separately with the vascular tissues of the corm. The roots extend in a general horizontal direction outward from the vascular tissue; three roots occur between the vascular tissue and the central pit, and run in a downward direction.



FIGS. 1, 2.—Fig. 1, diagram of longitudinal section through protocorm: *x*, position of apical cell; *c*, cylinder strands; *r*, root strands; *l*, leaf strands; Fig. 2, transverse section of protocorm, 3 mm. above bottom of pit: *lp*, leaf primordium; *fl*, petiole of functioning leaf; *c,c*, cylinder strands; *r,r*, root strands; *l,l*, leaf strands; ×7.

From study of the serial sections a model of the vascular system was built up in clay to a scale of 30 diameters. This was copied in plaster and photographed (figs. 3, 4, 5).

As shown by these figures, the vascular tissue makes up a definite cylinder. Its structure will be understood from the following illustration. Suppose the vascular cylinder of an ordinary rhizome of this species to be turned "wrong side out" by pulling the apical region down through the center of the stele, as one would pull the bottom of an inverted sack through the tubular part. This eversion of the stele of an ordinary rhizome of *O. vulgatum*

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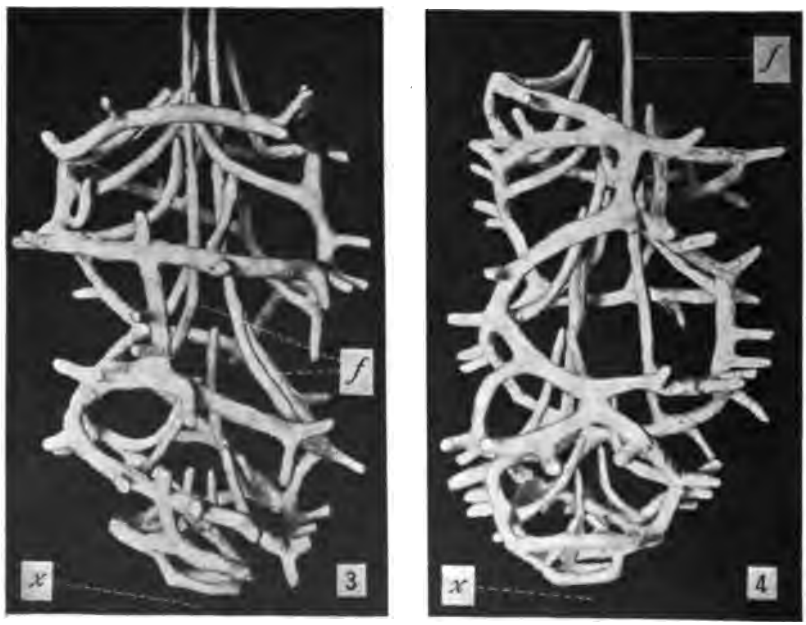
would produce a structure differing in only two important particulars from the vascular cylinder of the protocorm: (1) the leaf trace of the inverted cylinder of the rhizome would be a single bundle; the leaf trace of the protocorm consists of two bundles; (2) the roots of the everted cylinder of the rhizome would be within the cylinder; in the protocorm, with three exceptions, they are outside.



FIGS. 3, 4.—Fig. 3, model of the vascular system of the protocorm, from the side: *f*, bundles of the functioning leaf; *x*, position of apical cell; ×8; Fig. 4, model from the side at right angles to fig. 3.

As indicated by this illustration, the oldest portion of the cylinder is at the top of the corm and the formation of new vascular tissue proceeds in a downward direction. There is a gap in the cylinder corresponding to each leaf; no gaps not definitely related to leaves occur. The gap is below the point of attachment of the leaf bundles, as would be the case in the everted cylinder of a rhizome as described above. On either side of a gap a strand runs downward in a nearly vertical direction for a short distance

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and then divides into two strands which run almost horizontally and close the leaf gaps on either side. The leaf bundles corresponding to a gap sometimes attach to the vertical strands at the sides of the gap; much more usually, however, they connect with the horizontal strand above the gap, at about 90° apart.

In a single instance, three bundles separate from the strands of the cylinder. Two of these fuse at a very short distance from their points of connection with the cylinder strand, and the two resulting strands form the vascular supply of a leaf.

Along a vertical strand the phloem is upon the inside of the cylinder and the xylem outside (fig. 6). Where the strands run horizontally the phloem is often upon the upper side. This twist of the strands never exceeds 90°, that is, phloem never occurs on the outer side of a strand. The protoxylem is at the outer margin of the xylem area (fig. 7). No endodermis can be distinguished about any of the cylinder strands; both xylem and phloem are bordered directly by unmodified parenchyma.

FIG. 5.—Model from above

The leaf bundles, when they separate from the cylinder strands, run horizontally inward for a short distance, then run obliquely upward till they emerge within the central pit. At this point the two bundles of a leaf trace are about 0.5 mm. apart, and they run parallel to each other at this distance through that part of the petiole within the pit.

In the petiole of the leaf the xylem is adaxial, as in an ordinary plant. Where the leaf bundles are horizontal the phloem is above the xylem, and in this position the xylem and phloem connect directly with the corresponding tissues of the horizontal cylinder strands. In the few cases where a leaf strand connects with a vertical cylinder strand, the xylem connects directly. The phloem of the cylinder strand swings to one side to pass the xylem of the

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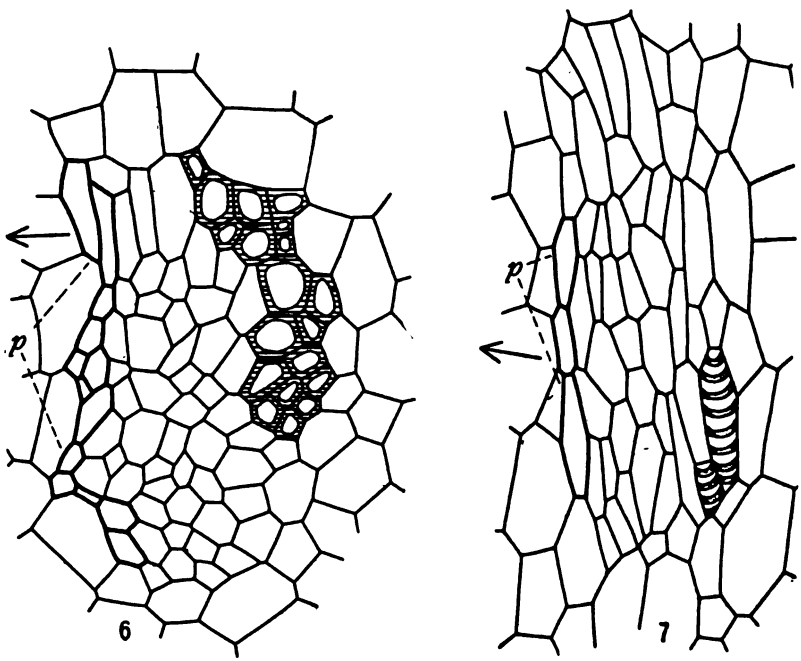
leaf strand and then connects with the phloem upon the upper side of the leaf strand.

The roots grow in a slightly downward direction outward from the vascular cylinder. The root stele is monarch with the phloem above, as described for the roots of this species. Where these attach to a horizontal strand of the cylinder, the xylem and phloem are in the same relative positions in the two strands, and they



FIGS. 6, 7.—Fig. 6, transverse section of cylinder strand of protocorm: arrow indicates direction of central pit; *p*, phloem; ×236; Fig. 7, diagonal section of young cylinder strand of protocorm: arrow indicates direction of central pit; *p*, phloem; ×236.

connect directly. Where a root connects with a vertical strand of the cylinder, the xylem of the root connects directly with that of the cylinder strand; the phloem of the root swings to the side of the cylinder strand and passes around to its inner side, where it connects with the phloem of that strand.

The roots are very numerous. There are about sixty-five in which xylem has been differentiated, and probably fifteen more in

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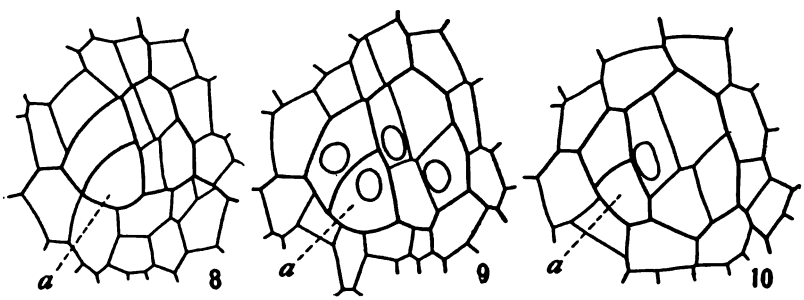
which root formation is evidenced by at least an apical cell. A root usually attaches to the cylinder near the point of attachment of a leaf bundle. This produces a cross of vascular tissue, such as is shown in fig. 2. This relation of leaf bundle to root bundle is not invariable.

The ground tissue of the protocorm is a large-celled parenchyma similar to that of an ordinary rhizome. There are no intercellular spaces. The tissue within the vascular cylinder differs in no way from that outside. The cells everywhere are packed with food material, principally starch.

Examination of the sections through the region immediately below the bottom of the central pit of the protocorm shows a



FIGS. 8–10.—Fig. 8, a transverse section of apical region of protocorm, 40 μ below bottom of central pit: *a*, apical cell; ×236; Fig. 9, a section 70 μ below bottom of pit; Fig. 10, a section 95 μ below bottom of pit.

conspicuous apical cell, triangular in cross-section (figs. 7, 8, 9). This apical cell is an inverted triangular pyramid with strongly curved faces. It is about 120 μ in length from vertex to center of base, and each side of the base is approximately 30 μ in length. By reason of the strong curvature of the faces of the pyramid, the cross-section of the cell is greatest about halfway between vertex and base, where each side of a transverse section measures about 42 μ.

The youngest segment of the apical cell has not divided. The next segment has divided twice longitudinally (figs. 8, 9, 10), and one of the resulting cells has divided once transversely, as shown by a count of the nuclei. The outlines of the third segment cannot be traced.

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When a segment is first cut off from the apical cell, its principal wall is approximately parallel to that of the apical cell. The lower portion of the segment soon enlarges and the segment assumes the shape of a truncated rectangular pyramid, with the smaller end above. Transverse sections of the second segment, as represented in figs. 8, 9, and 10, show this enlargement of the lower portion of the segment. This unequal growth of the upper and lower parts continues with the further division of the cells of the segment. The result of this unusual manner of growth is represented diagrammatically by fig. 11. As shown by this diagram, the upgrowth of the peripheral region and the resultant everted form of the protocorm are direct results of the behavior of the segments of the apical cell.

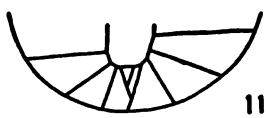

FIG. 11.—Diagram showing eversion produced by unequal growth of upper and lower portions of the apical segments.

For purposes of comparison, the apical region of an ordinary rhizome, already described by HOLLE (10), was re-examined with especial reference to the divisions of the segments of the apical cell. In all cases examined, the apical cell is a triangular pyramid, as in the protocorm; it measures 120–150 μ in length and 30–50 μ across each face at the point of greatest width (figs. 12, 13). Each segment divides transversely first, that is, by a periclinal wall. Two longitudinal divisions at right angles to each other usually follow in the outer cell of the segment. The inner cell of the segment may divide in the same way, but more usually the divisions are irregular. While the segments cannot be traced to any considerable distance from the apical cell, it is clear that the upper and lower parts of a segment enlarge about equally, in contrast to the unequal growth of the parts of the segment in the protocorm.

Leaves and the sheathing tissue about the leaf bases arise from the upper cell of the segment; stem tissue is produced by the lower cell. Procambium develops very near the apical cell, within the region where the segmentation can be definitely determined (fig. 13). In the case figured, it is certain that the vascular tissue of the stem is being developed directly from segments of the apical cell, and entirely independent of the leaf traces. The

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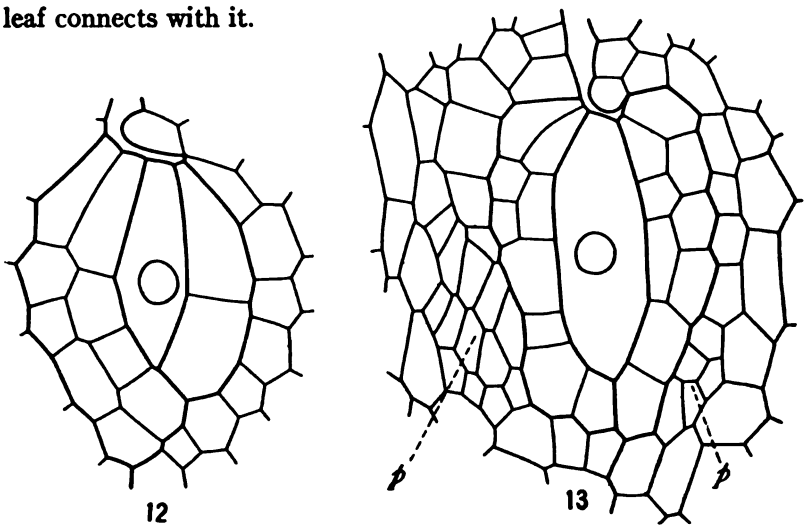
procambium strands figured, when traced through the serial sections, are found to connect. They constitute the vascular strand which closes the gap of the leaf second in order from the apical cell; the procambium of a trace which will supply the youngest leaf connects with it.



FIGS. 12, 13.—Fig. 12, longitudinal section through apical region of rhizome; ×236; Fig. 13, longitudinal section through apical region of rhizome: *p*,*p*, procambium strands; ×236.

Discussion

In view of the complex anatomy of the specimen investigated, it seems necessary to state that the term "protocorm" is used by LAND (11) and in this paper without any intended implication that the object so named is necessarily simple in its structure. The name has been applied rather with reference to its external appearance, which is not unlike that of mature plants of *Phylloglossum* and of young plants of *Lycopodium cernuum*, to which the name was first applied.

In order to compare the vascular system of the protocorm with that of an ordinary rhizome of the species, the effects of the unusual behavior of the segments of the apical cell must be taken into account. By reason of the eversion produced, the tissue surrounding the central pit corresponds directly to the cortex of an ordinary rhizome. In the same way, as regards origin, the tissue immedi-

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ately outside of the vascular system is pith. The xylem and phloem are therefore, for the most part, placed in the usual collateral arrangement, with phloem next to the cortex. The protoxylem occurs next to the pith. Hence we may describe the vascular system of the corm as an everted ectophloic siphonostele with endarch xylem. The vascular cylinder therefore differs from that of the rhizome only in being everted.

The constant occurrence of a double leaf trace in this specimen is noteworthy. Exactly the same situation has been described for *O. palmatum* by BOWER (3). The same writer (2) describes the leaf trace of *O. pendulum* as composed of five strands, and thinks it probable that this is the case in all the species of the group OPHIODERMA. If this be true, the specimen described in this paper represents the fifth species of the genus in which a multiple leaf trace occurs.

BOWER points out the fact that those species which have a multiple leaf trace are offshoots of the main line of the genus, and he considers them as derived forms. In the case under discussion, the specimen described belongs to the species usually considered most representative of the genus. It is to be noted that the rhizome of *O. palmatum* is very broad in proportion to its length, and often almost spherical in shape. While the rhizome of *O. pendulum* is relatively small, the figures of *O. simplex* indicate a rather stout stem, and CAMPBELL (8) describes the rhizome of *O. intermedium* as "very short, forming a small tuberous body." It seems probable that in the protocorm described above the doubling of the leaf trace is related directly to the extreme lateral expansion of the corm, due to its manner of growth; and it is possible that in the other species of this genus with a multiple leaf trace the same explanation may hold.

If this explanation of the doubled leaf trace is accepted, every unusual feature of the protocorm is definitely related to the peculiar behavior of the segments of the apical cell. It is to be noted that these segments in the protocorm differ in their development from those in the rhizome in two particulars: (1) in the rhizome the first division of a segment is transverse, and the later divisions are variable; in the protocorm the first two divisions are longitudinal;

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(2) in the rhizome the upper and lower parts of a segment develop uniformly; in the protocorm the upper and lower parts of a segment grow unequally and the eversion of the corm results.

CAMPBELL (8) states that in *O. moluccanum* there is "no reason for assuming that the tissues of the very open reticulum forming the fibrovascular system of the rhizome is in any part due to additions from the apical tissue of the stem." As pointed out above, this is distinctly not the case in the rhizome of *O. vulgatum*, where the procambium strands are definitely related to the apical cell. It is to be noted also that the procambium of a leaf trace develops first at the point of connection of the strand with the cylinder.

Summary

1. The protocorm is nearly spherical, with a circular pit in the center of the top. This pit extends downward about 0.8 of the diameter of the protocorm, and the apical cell is located at its bottom.

2. The bases of the leaves are attached to the sides of this pit, with the oldest at the top. The functioning leaf is the seventh, and the primordia of six others occur below it.

3. The vascular cylinder is an everted ectophloic siphonostele with endarch xylem. The leaf trace consists of two strands which attach separately to the cylinder. The roots are numerous and outside the cylinder.

4. The apical cell is a triangular pyramid. The segments divide twice longitudinally before a transverse division occurs. The segments enlarge below more rapidly than above, and the eversion of the cylinder results from this.

5. The segments of the apical cell of a rhizome of *O. vulgatum* divide transversely first; the later divisions are irregular. The upper and lower portions of a segment enlarge uniformly.

6. The vascular tissue of the rhizome is produced by the apical cell directly, and is not made up of leaf traces.

The writer is indebted to Professor JOHN M. COULTER for many helpful criticisms, and to Dr. W. J. G. LAND under whose direction the investigation was made. The writer wishes also to express his thanks to Mr. W. A. POYSER for help in securing material.

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CURRENT LITERATURE

BOOK REVIEWS

Soil fertility

RUSSELL[1] has added to the monographs on biological chemistry a volume on soil conditions and plant growth. The table of contents by chapters gives an idea of the scope of the work: (1) historical and introduction, (2) constitution of the soil, (3) carbon and nitrogen cycles of the soil, (4) biological conditions of the soil, (5) soil in relation to plant growth, (6) soil analysis and its interpretation. There is also an appendix on methods of soil analysis. The book contains a bibliography of 323 citations and an index of two pages.

The treatment of the subject deserves characterization as critical, broad, and in the main unbiased. The soil is considered as an environmental factor of the plant, as the title implies, and not merely from the side of chemical and physical analysis. Great emphasis is laid upon the application of BLACKMAN'S idea of limiting factors, a principle the importance of which in biological problems it is hard to overrate. In this connection the author cites data to show that addition of mineral salts has little or no effect on yield if another factor, such as water supply, is already a limiting factor. RUSSELL concludes that soil toxins play no part in the fertility of well cultivated and drained agricultural lands, but admits that they are formed and may remain for some time in poorly drained and "exhausted" land. Some will question whether he has sufficient data for such a sweeping statement in the face of some of the experiments of our Bureau of Soils. Many will commend the caution with which he uses the term "available nutrients," or in his terminology "available food," also his lack of readiness to distinguish sharply between "essential" mineral salts and other salts and even organic compounds that increase yield.

In spite of the breadth of treatment that characterizes the monograph in the main, and the evident attempt of the author to give every soil factor affecting growth and yield its proper emphasis, it is evident that he turns more often than our present knowledge will insure to deficiencies of some mineral nutrient as the limiting factor. For instance, he attributes increased yields due to heating soils or treating them with poisons to the increase in ammonium salts due to differential killing of soil organisms, thus furnishing a greater nitrogen supply. It is true that there is some questionable evidence

[1] RUSSELL, EDWARD J. (Rothamsted Experimental Farm), Soil conditions and plant growth. viii+168. London: Longmans, Green & Co. 1912.

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that such treatment leads to an increase in ammonium salts, but it is not shown that such an increase of ammonium salts, by furnishing more nitrogen, will cause such a rise in yield, nor that the beneficial effects are not due to any one of half a dozen other possible changes in the soil. BOLLEY has some evidence that in the wheat lands of North Dakota such treatment increases yield by killing certain parasitic fungi.

Since SCHREINER and his collaborators have shown that many organic substances, some toxic and some stimulative to higher plants, are produced by decomposition of the organic débris of the soil, it is possible that the effect here is due to accumulated organic substances of one sort or another brought about by unbalancing the soil flora or fauna. Our Bureau of Soils has also collected much other data showing the extreme complexity of the problem of fertility and the danger of reasoning too directly from the mineral nutrient theory.

There are a number of minor defects involving form of statement, degree of emphasis, and errors of fact (certain to creep into the most carefully written book) that deserve notice. Only a few of these can be mentioned. Considering the idea RUSSELL wishes to convey, it seems better to use the more specific term "mineral nutrient" than the word "food." The author considers that non-available water is such because of the concentration (osmotic activity) of the salts in it (p. 104). Known facts in this matter indicate clearly that the resistance to absorption is capillary. Rendering soil toxins innocuous by oxygenating or by filtering over fine powders is described as precipitating them (p. 133), whereas the process in the first case is oxidation and in the second adsorption. No mention is made of the importance of surface tension in soil phenomena, though it plays an important rôle in flocculation, deflocculation, localization of solutes, etc.—WILLIAM CROCKER.

The evolution of plants

This little volume by SCOTT[2] belongs to a not unfamiliar category, but it is rare to find a work on evolution written by an eminent morphologist and a distinguished paleobotanist. This constitutes such an unusual equipment that although the work under consideration is popular in its appeal, the mode of treatment is of interest to the professional botanist.

The author at the outset draws a happy parallel between the value of our knowledge of fossil forms as a key to the course of plant evolution in general and the history of cultivated varieties of plants in relation to their derivation from wild ancestors. In a second chapter the characteristics and statistics of the angiosperms are dealt with, special emphasis being laid on the external organization of the angiospermous flower. In the third chapter the gymno-

[2] SCOTT, D. H., The evolution of plants. pp. 256. *figs. 25.* New York: Henry Holt & Co. 1912. 75 cents.

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sperms are discussed, which as the author points out constituted the characteristic vegetation of the secondary or Mesozoic period, just as the angiosperms are of the present. Here, in accordance with the author's well known point of view, the Cycadophytes receive a very large amount of attention, to the practical exclusion of the actually as well as mesozoically much more important Coniferales.

Beginning with the living cycads, which are remarkably well summarized as to their characteristics and distribution, SCOTT continues with a description of the more important features of the mesozoic Cycadophytes, the Bennettitales. These are elaborated chiefly in connection with the hypothesis revived in recent years by WIELAND, that they are the direct ancestors of the angiosperms. Here the distinguished author, so well known for his anatomical investigations, pins his faith unreservedly to the externals of their reproductive structures. His summary of their angiospermous features is as follows: (1) the presence of flowers organized on the same general plan as the typical flowers of the angiosperms; (2) the formation of a fruit inclosing the seed; (3) the exalbuminous character of the seed. SCOTT concludes in regard to the Bennettitales and their supposed angiospermous affinities: "They have thus proved to fully deserve the name Proangiosperms, which SAPORTA, by a brilliant inspiration, gave to *Williamsonia* and *Bennettites*, at a time when their stucture was very imperfectly known." It is perhaps worth while to recall in this connection that ASA GRAY, who knew his Compositae perhaps better than any other person living, referred the genus *Williamsonia* with conviction to the Compositae. Apparently the reproductive structures of the Bennettitales may be quite as appropriately regarded as equivalent to the inflorescence of this high group of dicotyledons as that of the flower of the lower angiosperms. Surely here Homer nods!

One of the most interesting chapters is that in which the author deals with the fernlike seed plants, which he himself has done so much to rescue from oblivion and restore. With characteristic modesty he makes no reference to his own contributions in this interesting field. The Medulloseae are apparently now regarded as more nearly allied to the cycad stock than the Lyginodendreae, thus slowly reversing the opposite conclusion adopted by the author in earlier years.

The book concludes with chapters on the true ferns, the club mosses, and horsetails (together with sphenophylls), which latter SCOTT still prefers to associate with the fern stock. The closing remarks on the relation of the paleobotanical record to the general principles of plant evolution are of particular value, most of all the statement as to evolutionary progress being more frequently from the more to the less complex and not vice versa, as is too often assumed by writers on evolution. Would that SCOTT and other English morphologists might focus their attention on this principle in dealing with anatomical structures!—E. C. JEFFREY.

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The natural history of coal

There is perhaps no substance of vegetable origin of greater importance and intellectual interest than coal. Nevertheless, we are largely ignorant of its composition and mode of formation. What knowledge we possess is almost exclusively based on inferences drawn from the organization of the rocks lying above and below the actual coal beds. Obviously inferences derived from such data are as open to error as the judging of the character of a book from the nature of its bindings. The geologists have notably failed to give us any adequate description or explanation of this greatest of mineral products, and it is now obvious that we must look to the anatomist and the paleobotanist, in collaboration with the chemist and physicist, to clear up this literally as well as figuratively dark subject.

ARBER[3] has stated the problem in an admirably clear and succint way, and has interestingly summed up the history of our knowledge of coal to the present time, with indications of the probable lines of successful attack in the future. It is noteworthy that the greatest recent modifications of our views in regard to coal have come about from the successful preparation of microscopic sections of certain types by the French investigators BERTRAND and RENAULT. It is now realized that a considerable number of combustible minerals have been formed in open water, and are to a large degree composed of the remains of phytoplankton (autocthonous and allocthonous). This is notably the case with coals rich in gases and hydrocarbons, such as cannels, bogheads, oil shales, bituminous shales, etc. Our information in regard to the coals which are not bituminous, or at least not markedly so, is in a less advanced state on account of the impossibility until quite recently of securing sections of the coal substance sufficiently thin and decolored to show their organization. On this subject ARBER writes as follows: "If we prepare thin slices of coal, ... and examine them under the microscope, we shall find as a rule that they are very disappointing as regards the amount of information we can obtain from them. Such sections are usually opaque, even when quite thin, and the substance is obviously very homogeneous." Fortunately the difficulties here described have quite recently been almost entirely obviated, for it has been found possible to prepare fairly thin and translucent sections even by the grinding method used by the petrographer, and by a modified biological technique it becomes feasible to prepare transparent slices of practically all categories of coals.

The writer shows that the old chemico-physical hypothesis of the origin of the various categories of coal, the peat-to-anthracite theory, is no longer tenable, but must be replaced as our knowledge permits by biological and biochemical hypotheses. The nature of a coal, where we are at present acquainted with its real composition, depends as much as anything on the

[3] ARBER, E. A. NEWELL, The natural history of coal. Cambridge Manuals of Science and Literature. pp. 163. *figs. 21.* Cambridge University Press. 1911. 1s.

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character of the plant remains which compose it, and to a much less degree on the chemical and physical conditions to which it has subsequently been exposed. It is accordingly clear that the study of coal is to a very large extent within the domain of the biologist, for certainly no adequate conception of the problem can be reached without his cooperation.

There are a few slips on the part of the author; for example he states that anthracite and cannel differ from ordinary so-called bituminous coal and oil shale or boghead respectively, by the fact that they contain little or no ash. Obviously this statement does not generally hold of these types of coal as mined in North America. ARBER has confined his observations in this respect to European coals. His book is nevertheless planned on the broadest lines, and is commended to all who wish to obtain a clear conception of our present knowledge of coal.—E. C. JEFFREY.

NOTES FOR STUDENTS

Recent work in gymnosperms.—In 1910 SCOTT and MASLEN established the genus *Mesoxylon* to include certain paleozoic stems intermediate in structure between *Poroxylon* and *Cordaites*, giving diagnoses of five species. One of these (*M. Sutcliffii*) has been described in detail by MASLEN,[4] and now two more species are described by SCOTT.[5] The conclusion is reached that *Mesoxylon* is "the last link in the chain of fossil types connecting the Pteridosperms with the typical *Cordaites* of the Upper Paleozoic," being definitely distinguished from it only by the presence of centripetal xylem in the stem. A critical discussion of the relationships of the new genera recently established by ZALESSKY is also given.

Mrs. THODAY and Miss BERRIDGE[6] have made an anatomical investigation of the strobili of four species of *Ephedra* (*E. altissima*, *E. distachya*, *E. fragilis*, *E. nebrodensis*). The "clearly bifid" stamen of the three last named species, each half bearing four bilocular synangia, is traced into other species in which the bifid character is not evident, but in which there are fusions of synangia into trilocular or even quadrilocular synangia, until *E. altissima* is reached with only two bilocular synangia. A reduction series is also traced from the staminate disk of *Cycadeoidea*, through other disks of Bennettitales, to *Ephedra*, where the disk is reduced to two segments, each bearing two pairs of bilocular synangia, and to *Welwitschia*, with its disk of six segments bearing trilocular synangia. It is also discovered that the solitary ovule of the species investigated is the product of a fusion of the two ovules of the biovulate species, since

[4] Rev. in BOT. GAZ. **52**:326. 1911.

[5] SCOTT, D. H., The structure of *Mesoxylon Lomaxii* and *M. poroxyloides*. Ann. Botany **26**:1011–1030. *pls. 87–90*. 1912.

[6] THODAY (SYKES), MARY G., and BERRIDGE, EMILY M., The anatomy and morphology of the inflorescences and flowers of *Ephedra*. Ann. Botany **26**:953–985. *figs. 21. pl. 85*. 1912.

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E. altissima revealed a long series of intermediate forms. This suggests that the solitary ovule of *Ephedra* and of *Welwitschia* represents a fusion of "the many ovules and interseminal scales of such a flower as *Cycadeoidea*."

THOMPSON[7] has attacked the problem of the affinities of the Gnetales with the anatomical weapons forged in the study of the conifers and the primitive dicotyledons. In this first paper the genus *Ephedra* is considered, the anatomical features being described in detail. The idea that *Ephedra* may be connected with the Bennettitales or the Cycadales receives no support from the anatomy; on the contrary, the suggestions of relationship to the Coniferales are numerous (arrangement of primary vascular bundles, double leaf trace, arrangement and structure of the tracheid pits, bars of Sanio, tertiary spirals, trabeculae and resin plates, primitive uniseriate lignified rays, wood parenchyma, and endarch leaf bundles). It is further evident that the group could not have arisen from any of the modern conifers, but rather "from or close to the base of the coniferous line." An angiospermous affinity is indicated clearly "by the possession of true vessels, broad rays, formation of broad rays by fusion, and separation of the leaf traces." These general conclusions are abundantly confirmed by the morphological evidence.

Miss BERRIDGE[8] has discovered that a ring of complex groups of vascular strands arises from the bundles in the base of the ovulate "flower" of *Gnetum Gnemon*, and suggests that this may indicate that the ovule was "primitively surrounded by a whorl of male flowers." This would mean that the ovulate strobilus of *Gnetum* was originally bisporangiate.—J. M. C.

Evolution of araucarians.—Probably the most discussed question in connection with the phylogeny of conifers is the relationship of the araucarians to the Abietineae. So far as the historical evidence goes, the two tribes are rivals in age, and the araucarians seem to have been the dominant coniferous vegetation during the Mesozoic. The complete separation of araucarians from Abietineae, by suggesting either their direct origin from the Cordaitales or even from club-mosses, is an idea that has entered into the discussion.

JEFFREY has been a staunch defender of the primitive character of the Abietineae, and of the derivation of the araucarian type from this stock. In a paper just published,[9] he attacks the problem of the evolution of the araucarian type on the basis of a study of abundant material of the existing forms, which is compared critically with the mesozoic material. So far as the evidence of history and anatomy goes, the whole series, from the abietineous stock to

[7] THOMPSON, W. P., The anatomy and relationships of the Gnetales. I. The genus *Ephedra*. Ann. Botany **26**:1077–1104. *figs. 2. pls. 94–97.* 1912.

[8] BERRIDGE, EMILY M., The structure of the female strobilus in *Gnetum Gnemon*. Ann. Botany **26**:987–992. *figs. 4.* 1912.

[9] JEFFREY, E. C., The history, comparative anatomy, and evolution of the *Araucarioxylon* type. Proc. Amer. Acad. **48**:531–571. *pls. 7.* 1912.

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the living araucarians, becomes evident. Throughout the investigation it is assumed that the appearance of a character in response to wounding means the recall of an ancestral character.

The combination of characters that makes the araucarian wood unique among living conifers is the close-set and alternating pits of the tracheids, the absence of the bars of Sanio, the usual absence of wood parenchyma, and the much restricted pitting of the ray cells. The wound reactions obtained from living araucarians, combined with the structure and wound reactions of mesozoic forms, lead to the conclusions that the ancestors of the existing araucarians were characterized by the presence of wood parenchyma and by strongly pitted rays. Both of these features are inconsistent with direct derivation from the Cordaitales. The living araucarians have retained in the cone axis, root, and first annual ring of vigorous branches, the characteristic features of the mesozoic forms. It is further shown that the characteristic pitting of the tracheids of *Araucaria* and *Agathis* is not ancestral, but acquired. A very significant result is that obtained from a study of the resin canals, which shows that certain mesozoic araucarians possessed traumatic resin canals; and even in a living *Agathis* normal resin canals were found in certain peripheral regions.

The general conclusion is reached that the araucarians are not derived from the Cordaitales, since their primitive forms possess a number of features that have not been discovered among the Cordaitales. The araucarian type is derived from ancestors with opposite (not alternate) pitting, bars of Sanio, strongly pitted rays, and horizontal and vertical resin canals. This group of ancestral characters selects *Pityoxylon* as the ancestral abietineous type. There seem to be no question that the araucarian and abietineous stocks blend characters in the Mesozoic, and that recognizable araucarians started with numerous abietineous characters that gradually disappeared, until the existing araucarians are very distinct.—J. M. C.

Induction of inheritable changes in plants by ovarial injections.—FIRTH[10], in an apparently preliminary paper, has given the results of experiments, carried on in the hills of India, wherein it was attempted to produce "mutations" by the injections of different salts into the ovaries of plants, and also by the use of external conditions in the medium, and the adding of salts to the soil water. Pure cultures of *Oenothera Lamarckiana*, *O. tetraptera*, *O. odorata*, *Epilobium parviflorum*, *E. cylindricum*, and *E. hirsutum* had been kept in the garden and grown in "pure pedigreed strains" from 1906 to 1908. These were subjected to different experimental conditions of light relations, temperature relations, soil relations, and the injection of salts into the ovaries. Positive results seem to have been obtained in *E. parviflorum* when watered

[10] FIRTH, R. H., An elementary inquiry as to the origin of species. Jour. Royal Army Medical Corps **16**:497–504. 1911.

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with solutions of nitrate of potassium, in one series, which gave seeds, from which plants were grown "in which the stem and leaves were marked by very shaggy hairs, the leaves were definitely stalked, not sessile, distinctly stem-clasping, in shape ovate, with large sharp teeth." The new form, which did not conform to any known type, was carried "successfully" to the second generation but not beyond. These experiments were repeated in 1909–1910 but gave negative results.

Injection of salts into the ovary before fertilization, in dilutions of 1:1000, showed many failures by killing the "unfertilized ovules." Sodium chloride, nitrate of potassium, carbonate of ammonium, sulphate of sodium, and sulphate of iron were used. One series in which sodium chloride and carbonate of ammonium were injected into the ovaries of *E. roseum* showed "a number of aberrant forms of quite unknown type." "Three of the new forms were brought to bloom and maturity, and in one case to a second generation."

O. Lamarckiana when injected did not show any increased array of new types, but *O. odorata*, after the injection of carbonate of ammonia, produced a "bloom" "which reminded one strongly of *O. gigas*." It was sterile. In *E. hirsutum* only injections of nitrate of potassium gave results, and in one series there resulted a form that had many of the "features of another genus, namely *Circaea*," which reverted to the type of the parents in subsequent generations.

Apparently the paper is a preliminary announcement, and one regrets that it is not accompanied by illustrations and more data of the experiments and less of the general discussion of the problems. The chief interest in the paper lies in the fact that FIRTH apparently did not know of MACDOUGAL'S investigations along the same line, nor of the experiments of HUMBERT upon *Silene noctiflora*. FIRTH used the same methods that have been used by MACDOUGAL, but somewhat stronger solutions, and his results are an important confirmation of the general results obtained and methods employed by MACDOUGAL.—W. L. TOWER.

Effect of neutral salts upon plants and animals.—OSCAR LOEW[11] has investigated the effects of neutral salts upon the lower animals and plants. He finds that a 0.2 per cent solution of di-potassium oxalate more poisonous to infusoria than a 1 per cent solution of di-potassium tartrate. Infusoria, copepods, and rotatoria, which are able to live 24 hours (and some 3 days) in a 0.5 per cent di-potassium tartrate, die in 30–40 minutes in a 0.5 per cent solution of di-potassium oxalate. Seedlings of radish, clover, and barley, with root length of 1–3 cm., exposed to 0.5 per cent of the oxalate at a temperature of 12°–15° C., show loss of turgor in the root cells within 24 hours, and decay immediately follows, while in an equimolecular solution of the tartrate or a

[11] LOEW, OSCAR, Über die Giftwirkung von Oxalsaurensalzen und die physiologische Funktion des Calcium. Biochem. Zeitschrift **38**:226–243. 1912.

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0.5 per cent solution of sodium nitrate, they suffer little or no injury. Pea seedlings die in 2 days in a 0.5 per cent of sodium oxalate, but are still uninjured in an equally strong solution of sodium acetate.

In *Spirogyra* the first structure to show the effect is the nucleus, which contracts and becomes lens-shaped. A little later the chloroplasts begin to contract. LOEW finds that the effect is not due to acidity, since 0.005 per cent of oxalic acid is more injurious than 0.01 per cent of citric acid, and 0.0001 per cent more injurious than 0.001 per cent of tartaric acid.

LOEW concludes that the injurious effect of the oxalates is due to the extraction of calcium from the nucleoproteins, chromatin, and plastin, and its replacement by potassium or some other element, and their bringing about a change in the imbibing power of the different parts of the protoplasm. He thinks that calcium is an essential element in the cells of the higher animals and plants.—J. N. MARTIN.

Sutcliffia.—Miss DE FRAINE[12] has made a painstaking investigation, by means of the well known wax plate method of modelling, of the vascular system of *Sutcliffia*, a new genus of the Medulloseae established by SCOTT. Unfortunately the specimen is rather badly dilapidated and for that reason a certain reserve is necessary in interpretation. The vascular system as described by Miss DE FRAINE consists of a large axial "protostele" (sic!) surrounded by three more or less clearly identifiable "meristeles." In addition to these are a number of "extrafascicular" bundles. By a process of reasoning which it is difficult to follow, the author identifies the central "protostele" with the ring of bundles in the Cycadales. It would seem to be in accordance with the general principles of vascular anatomy to regard it as a medullary bundle, and the three surrounding strands as corresponding to the cylinder system of bundles, a conclusion rendered extremely probable by the fact that it is with these that the leaf traces become continuous. *Sutcliffia* is considered to be a primitive type regardless of the fact that it has an extremely multifascicular foliar supply. This would appear to be entirely against all established principles of anatomy. It is gratifying to find that English authors are gradually coming around to the standpoint in regard to the affinities of the Cycadales, namely as rather with the Medulloseae than the Lyginodendreae, which has been held in continental Europe and this country for more than a decade.—E. C. JEFFREY.

Cause of leaf fall.—In a limited series of experiments conducted with detached twigs of various deciduous trees placed in water in a saturated atmosphere, VARGA[13] has attempted to establish the relationship between this

[12] DE FRAINE, E., On the structure and affinities of *Sutcliffia*, in the light of a newly discovered specimen. Ann. Botany **26**: 1031–1066. *figs. 19. pls. 91, 92.* 1912.

[13] VARGA, OSKAR, Beiträge zur Kenntnis der Beziehungen des Lichtes und Temperatur zum Laubfall. Oesterr. Bot. Zeitschr. **61**: 74–88. 1911.

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phenomenon and the processes of transpiration and photosynthesis influenced by various conditions of light and temperature. These experiments seem to show that (1) any decided checking of photosynthesis either from light conditions or from a deficiency of carbon dioxide brings about leaf fall; (2) any lowering of transpiration also produces defoliation, but less rapidly than decreased photosynthesis; (3) variation in the intensity and quality of the light has no direct specific action upon leaf fall; and (4) lower temperatures are efficient in causing leaf fall through decreased photosynthesis and transpiration only within limits which permit the activities involved in the development of the absciss layer; below these limits the leaves die, but cling rather persistently to the twigs. It is to be regretted that the experiments were so limited and hence so few data were accumulated in support of the conclusions reached.—GEO. D. FULLER.

The Forest Club Annual.—Among the publications which tend to promote an intelligent interest in the problems of forestry this annual[14] from the University of Nebraska is worthy of something more than passing notice. Among the articles it contains are "Grazing investigations on our national forests," by A. W. SAMPSON, and "Effects of forests upon run-off in the Rockies," by R. D. GARVER. Both present data that are important from the ecological as well as the economic point of view. The same may be said of "Notes on winter-killing of forest trees," by C. P. HARTLEY, which shows the need of careful investigation of the various physical factors involved before any adequate explanation of the action of winter conditions upon forest trees may be obtained. The other problems discussed include forest conditions in parts of Nebraska and Arkansas, forest roads, trees suitable for streets and parks, and some phases of lumber manufacture.—GEO. D. FULLER.

Fairy ring fungi.—These well known fungi are found by BAYLISS[15] to be parasitic upon the roots of grass. They soon kill the roots by the secretion of some toxic substance. The same or some other secretion is toxic to the fungi themselves, making them unable to grow in the same soil for three years in succession and hence producing the well known development of yearly widening rings. Contrasted with the infected grass, that which lies immediately outside as well as inside the ring is stimulated into better growth by the greater abundance of nitrogenous food made available by the action of the mycelium of the fungi in secreting proteolytic enzymes. The yearly increase in the radii of the rings of *Marasmius oreades* was found to be 6–14 inches. —GEO. D. FULLER.

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[14] The forest club annual, vol. 4, pp. 160. University of Nebraska, Lincoln, Neb. 1912.

[15] BAYLISS, JESSIE S., Observations on *Marasmius oreades* and *Clitocybe gigantea* as parasitic fungi. Jour. Econ. Biol. 6:111–132. 1911.

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INHERITANCE OF FLOWER SIZE IN CROSSES BETWEEN SPECIES OF NICOTIANA[1]

E. M. EAST

(WITH PLATES VI–X)

Since the independent investigations of NILSSON-EHLE and of the writer demonstrated the feasibility of using the Mendelian notation to describe the inheritance of size characters that blend in the first hybrid generation, a number of botanical papers have appeared that supported this interpretation. These papers have considered the behavior in crosses of such characters as height of plant, size of leaf, number of leaves, time of flowering, and size of fruit. If the number of leaves in certain plants is excluded, this type of character is one particularly affected during development by external conditions. Since fluctuations produced in this manner are not transmitted, if the conclusions drawn from the sum total of our limited experimental cultures are to be given weight, the validity of the evidence in these investigations is not disturbed. At the same time, one must admit that these fluctuations obscure an analysis of the crude data. For example, plant *B* may be six inches higher than plant *A* when both are grown in the same environment, owing to a different heritage, but plant *A* may grow considerably higher than plant *B* if the environment of *A* is the best possible for maximum growth and the environment of *B* is poor.

In this paper, therefore, I propose to consider the inheritance of

[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

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a character-complex which I believe to be the least affected by external conditions of any character that shows marked varietal differences. This character-complex is corolla size. The fact that corolla size is so comparatively constant under all conditions attending development has such a definite bearing on some broad questions of organography that it merits separate discussion. On this account, the liberty of asserting the truth of the statement with only the following data in its support is requested.

During the past four years, I have grown about 20 species of *Nicotiana* in considerable numbers. They have been grown under very diverse conditions. Some have been starved in four-inch pots, others have had the best of greenhouse treatment; some have had poor field conditions, others have had all field conditions practically at their best. The height of the plants, the size of the leaves, and similar size complexes have varied enormously, but the size of the corollas has scarcely varied at all. For example, plants of *Nicotiana silvestris* Speg. and Comes grown to maturity in four-inch pots produced no leaves longer than 7 in. On the other hand, sister plants of the same pure line produced leaves 30 in. long in the field. Both series, however, produced flowers with the same length and spread of corolla. Furthermore, cuttings from 20 of the field plants reported in this study were rooted and grown in small pots in the greenhouse. Their blossoms were the same size as those of the field grown plants from which they came.

The material used in this particular experiment consisted of pure lines of two *Nicotiana* types that are generally treated as distinct species (pl. VI). The male parent was *Nicotiana alata grandiflora* Comes, it being the plant called *Nicotiana affinis* by horticulturists. Three lots of it were under observation; one was obtained from Italy and the other two from the United States, but the original sources of the strains are unknown. These three lots were alike, and in successive generations were constant in their characters. They accorded perfectly with COMES' description and were remarkably narrow in their variability. The female parent I have called *Nicotiana forgetiana*, Hort. Sand., and thereby hangs a tale. I found in the Gray Herbarium of Harvard University a sheet from near Los Angeles, California, marked *Nicotiana clevelandii* Gray.

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This designation was manifestly incorrect, as the plant was exactly like SANDER's figure of *N. forgetiana* in the *Botanical Magazine* (No. 8006). As it had been collected only a few years, I took seed from one of the capsules and planted it. It grew and again produced plants like *N. forgetiana*. Miss DAY, the librarian of the Gray Herbarium, then looked up the correspondence regarding the specimen and found that it was evidently a garden specimen grown by a Californian botanist, since deceased, from seed furnished by Sander & Sons and called *N. Sandarae*. The plants have not the mixed colors and the variability of the specimens now sold as *Sandarae* hybrids, but are constant in their characters and are identical with *Nicotiana forgetiana*. I have come to the conclusion, therefore, that I have obtained (as LOCK[2] probably did) seeds of the real *N. forgetiana* that had been mixed with the *Sandarae*[3] hybrids by Sander & Sons.

In view of the fact that *N. alata grandiflora* and *N. forgetiana* do not differ essentially in their foliage and habit of growth, but only in flower size and color—the one being white, the other red—perhaps one should not call them two species. I hold no brief either way. I simply accept the taxonomic ruling. At least, there existed here two strains very different from each other and very constant in their characters. Both were self-fertile, and in fact were usually self-pollinated naturally. They were crossed. There was no trouble about this, as every cross attempted was successful, and the capsules were filled with seeds.

This, then, seemed to be an excellent opportunity for studying size inheritance: two strains, uniform in pure lines, one with a corolla three times the length of the other, could be crossed easily. All was not plain sailing, however, for the plants of the F_1 generation (pl. VII) were absolutely self-sterile. This fact would have cut off the experiment in the flower of a promising youth but for the further fact that each plant was perfectly cross-fertile with every other plant. It did indeed reduce my interest in the inheritance of corolla size, for it precluded the study of an F_3 generation, but this was offset by the more fascinating problem of self-sterility.

[2] Ann. Roy. Bot. Gard. Peradeniya 4:195–227. 1909.

[3] The *Sandarae* hybrids were supposed to have been produced by the cross *N. forgetiana* × *N. alata grandiflora*.

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It was impossible to study the F_3 generation because crosses between two F_2 individuals alike somatically would be without meaning, since nothing could be known of the gametic potentiality of each. Crosses between F_1 individuals, on the other hand, meant something, because they were alike gametically. Six F_1 crosses were made therefore, and from them were grown 828 plants.

TABLE I

FREQUENCY DISTRIBUTIONS FOR LENGTH OF COROLLA IN A CROSS BETWEEN *Nicotiana forgetiana* AND *N. alata grandiflora*

Designation	Class centers in millimeters														
	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
N. forgetiana, 314	9	133	28	..	...	...	...	...	...	..	..	..	..	..	..
N. alata gr. 321	..	...	..	..	...	...	...	...	...	1	19	50	56	32	9
F_1 (314×321)	..	...	..	3	30	58	20	...	...	..	..	..	..	..	..
F_2 (314×321) 1–6	..	5	27	79	136	125	132	102	105	64	30	15	6	2	..

Table I shows the frequency distribution for length of corolla of *N. forgetiana* (314) inbred, *N. alata grandiflora* (321) inbred, the F_1 generation (314×321), and the F_2 generation (314×321) 1–6. The measurement was taken from the end of the pedicel to the center of the contraction commonly known as the corolla throat. The classes have a magnitude of 5 mm. and are centered at the even centimeters and half-centimeters. A glance at the distributions themselves is sufficient to show the small variability of the parent types and of the F_1 generation, and the great variability of the F_2 generation. The F_1 generation is strictly intermediate, as is the mean of the F_2 generation. *Among the individuals of the F_2 generation, however, are flowers identical with each parent.* This last fact is perhaps more clearly shown in the figures of pls. IX and X.

The statistical constants for each frequency distribution are shown in table II.

The spread of the corolla, measured to the tips of alternate lobes, behaved in the same way. Corolla breadth in *N. forgetiana* varied from 25–35 mm., with a sharp mode at 30 mm. The corolla spread of *N. alata grandiflora* was somewhat more variable in terms of the arithmetical standard, ranging from 55 mm. to 80 mm. The range of the F_1 individuals extended from 45 mm. to 55 mm.

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In the F_2 generation plants were produced with a corolla breadth identical with each parent. In fact, there were four individuals as small as the smallest specimens of N. *forgetiana*, and there was one individual with flowers within 3 mm. of the size of those of the largest *N. alata grandiflora* growing in my cultures. The mean of this distribution was 48.57 ± 0.19 mm., the standard deviation 8.07 ± 0.13 mm., and the coefficient of variation 16.62 ± 0.28 per cent.

TABLE II

STATISTICAL CONSTANTS FOR FREQUENCY DISTRIBUTION OF TABLE I

Designation	Mean	Standard deviation	Coefficient of variation
N. forgetiana, 314	25.6 ± 0.12	2.27 ± 0.08	8.86 ± 0.33
N. alata gr., 321	78.8 ± 0.28	5.38 ± 0.20	6.82 ± 0.25
F_1 (314×321)	44.3 ± 0.23	3.67 ± 0.17	8.28 ± 0.38
F_2 (314×321) 1–6	49.9 ± 0.26	11.26 ± 0.19	22.57 ± 0.39

Examination of the F_2 generation of this cross indicated a correlation between the length of the corollas and the lengths of the filaments and the styles that for all practical purposes was perfect. By this statement I mean that the anthers were invariably just above the stigmas and the stigmas were invariably at the throat of the corolla. Of course absolute measurements would not show an integral coefficient of correlation, nevertheless one may assume, I think, that the fact is simply obscured by slight fluctuations. It seems as if the numbers were adequate from which to conclude either that the determiner or determiners of corolla length are also determiners of the length of the style and the filament or that these factor complexes are perfectly coupled in inheritance.

Corolla spread is also correlated with corolla length. It is by no means uncommon to find a sharp break in the correlation, as is witnessed by the individual with the very broad corolla and comparatively short tube pictured in pl. X, fig. 8; but one never finds inverse extremes in the same individual. Just what the correlation coefficient 0.610 ± .015 would prove to mean if individual analysis of later generations were made, is doubtful. We cannot go back of the gross statement that such a correlation exists

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in the general population. Perfect coupling of certain factors together with independent combination of others may be possible; partial coupling arising from a peculiar gametic distribution may be equally possible.

TABLE III

CORRELATION BETWEEN LENGTH AND SPREAD OF COROLLA IN F_2 GENERATION OF CROSS BETWEEN *N. forgetiana* AND *N. alata grandiflora*

Breadth of corolla in millimeters

Length of corolla in millimeters	25	30	35	40	45	50	55	60	65	70	75	
25	1	...	4	...	...	...	...	...	...	...	...	5
30	2	5	4	10	3	3	...	...	...	...	...	27
35	1	5	17	26	21	6	3	...	...	...	...	79
40	...	6	12	38	41	31	7	1	...	...	...	136
45	...	...	8	20	29	31	26	8	2	1	...	125
50	...	...	3	22	30	44	25	7	1	...	...	132
55	...	...	1	2	22	27	37	9	4	...	...	102
60	...	...	1	3	11	32	29	19	9	1	...	105
65	...	...	...	...	6	17	21	12	7	1	...	64
70	...	...	...	1	1	5	15	4	4	...	...	30
75	...	...	...	...	...	7	3	4	...	1	...	15
80	...	...	...	...	...	1	1	3	...	...	1	6
85	...	...	...	...	...	1	...	...	1	...	...	2
	4	16	50	122	164	205	167	67	28	4	1	828

Coef. cor. 0.610 ± 0.015

These are the principal facts collected regarding this cross, if the small leaf differences and other minor variations are left out of consideration. How unimportant the latter are, can be seen by a reference to pl. VIII. There are several suggestions that may be made regarding the simple facts obtained, however, that may be helpful in further Mendelian interpretations of size complexes.

Elsewhere[4] it has been shown that the behavior of such characters in crosses is adequately represented by the segregation and

[4] Amer. Nat. 44:65–82. 1910.

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recombination of cumulative unit factors that do not show the phenomenon of dominance. The frequency distribution of the F_2 generation in these cases is not $(\frac{3}{4}+\frac{1}{4})^n$, as it is where dominance is complete, but is $(\frac{1}{2}+\frac{1}{2})^{2n}$, because a factor in the heterozygous condition is to be regarded as producing one-half the effect that it produces when in the homozygous condition.

Regarding this expression as proper for the moment, let us examine the F_2 frequency distribution for length of corolla with the idea of assigning a definite number for n in the expression $(\frac{1}{2}+\frac{1}{2})^{2n}$.

If n is made equal to 3, then by the theory the F_2 distribution should have seven classes with the frequencies

1–6–15–20–15–6–1

per 64 individuals. For 828 individuals, the grandparental sizes should each be recovered $(828 \div 64) = 13.0-)$ nearly thirteen times. This was not the case in the actual distribution.

If n is made equal to 5, the F_2 distribution should have eleven classes with the frequencies

1–10–45–120–210–252–210–120–45–10–1

per 1024 individuals. With 828 individuals the grandparental classes should each be recovered only 0.8 times; in fact, a majority of populations of this size would not show the grandparental classes at all. This also is not the condition that was actually found.

There is left only the possibility of making n equal to 4. When this is done the F_2 distribution for 256 individuals—the smallest number in which a representative of each class may be found—and for 828 individuals is as follows:

1 – 8 – 28– 56– 70– 56– 28– 8– 1
3.2–25.9–90.6–181.1–226.4–181.1–90.6–25.9–3.2

This calculation points to the recovery of each grandparent about 3 times in the F_2 population under observation. Reference to table I shows that the figures actually obtained agree rather closely with this observation. But table I also shows another important fact. The arbitrary classes used had a range of 5 mm., which makes 13 classes necessary to express the F_2 generation.

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This class size was adopted in accordance with the usual biometrical procedure, the variations in the small parent (314) being included in only 3 classes. But when this is done, the F_2 distribution is decidedly skew. The theoretical mode is along about the fourth or fifth class instead of the central class. What is the reason for the production of this type of curve? There must be a reason, and it seems to me that this reason must be biological and not a mathematical transnomination, as have been all the biometrical analyses of skew curves. The matter appears clear in the light of the following interpretation.

In ordinary statistical work, one produces a frequency distribution by throwing his tabular entries into arbitrary classes of equal size. By this procedure he has in all probability distorted their relationship. This fact is partially recognized by using the coefficient of variability instead of the standard deviation as a measure of variation. Unfortunately, it is usually said that the coefficient of variability is used instead of the standard deviation because it is an abstract measure and pounds can be compared with inches, etc. Standard deviations in the same concrete terms are usually thought comparable with each other. But is this true? Apply the rule to the data in tables I and II. The range of length of corolla of *N. forgetiana* (314) is 3 classes, the standard deviation is 2.27 ± 0.08 mm., and the coefficient of variability is 8.86 ± 0.33 per cent. The range of *N. alata grandiflora* (321) is 6 classes, its standard deviation is 5.38 ± 0.20 mm., and its coefficient of variability is 6.82 ± 0.25 per cent. Comparing standard deviations, *N. alata grandiflora* is twice as variable as *N. forgetiana*. Comparing coefficients of variability, which being functions of the mean give weight to the size of the mean, the large-flowered type (321) is less variable than the small-flowered type (314).

Let us now look at the matter from an ordinary common-sense biological standpoint. These pure line populations may be considered as composed of near-homozygous individuals. The range of variability shown is therefore almost wholly due to environment. In general, *N. alata grandiflora* has a corolla more than twice as long as *N. forgetiana*. Is it not reasonable to suppose that the unit change effected by environment and expressed as a

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fluctuation is proportional to the size of the individual? Is it not true that favorable circumstances which force the corollas of *N. forgetiana* to become 5 mm. longer than usual will produce a 10 mm. change in *N. alata grandiflora?*

If this is the correct way of looking at these two cases, then it is assuredly an error to plot the F_2 distribution—which includes both grandparental sizes—in classes of equal size. Assuming that our hypothetical size factors affect the individual as growth forces, it seems probable that they are not only cumulative but accelerative. Roughly one might imagine the effect on the individual to be something like a constant percentage. I do not believe these cases of size inheritance can be analyzed into their component factors and these factors given their proper weight (using the word factor in the general sense of elements or causes that produce a result) sufficiently well to give a precise value to the character determiners themselves. On the other hand, it is interesting to see just what is necessary in the way of class range to bring our F_2 corolla distribution to the normal distribution for four factors ($n=4$). Fortunately the corolla sizes were taken by millimeters, so this can be done. First I have smoothed the figures according to the regular method. The distribution in one-millimeter classes is then as follows (table IV, p. 186).

Suppose now we begin at 24 mm. and take for this class a range of 4 mm. Then let us increase our class range 1 mm. each time. This gives a simple arithmetical progression with an advancing difference of the second order, that is, the differences between the class ranges are constant. Compare the frequency distribution thus obtained with the expansion of $(\frac{1}{2}+\frac{1}{2})^{2n}$ where n is equal to 4. This is done in table V, with an agreement among the figures that is very remarkable. If I were a biometrician, I probably could show that this agreement could not be due to chance—since by chance it could only occur once in some hundreds of thousands of times—and must therefore have some great significance. I should prefer to believe that I happened by chance upon a series of class ranges that fitted the normal frequency theory. But it must be emphasized that it was a *constant* increase in class range that produced the normal curve from the distorted skew curve.

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Perhaps no two actual frequency distributions would be alike in thus yielding to a simple arithmetical correction. Such a correction is probably fallacious in its simplicity. It serves our purpose,

TABLE IV

MEASUREMENTS OF LENGTH OF COROLLA IN F_2 POPULATION OF CROSS BETWEEN *Nicotiana forgetiana* AND *N. alata grandiflora*

Size mm.	freq.	Size mm.	freq.	Size mm.	freq.
24	0	45	25	66	12
25	2	46	28	67	10
26	2	47	29	68	7
27	2	48	28	69	7
28	1	49	28	70	6
29	3	50	26	71	6
30	5	51	28	72	5
31	8	52	23	73	6
32	10	53	20	74	4
33	11	54	20	75	3
34	15	55	19	76	2
35	13	56	22	77	2
36	18	57	22	78	0
37	18	58	22	79	1
38	19	59	26	80	2
39	26	60	21	81	2
40	28	61	22	82	1
41	33	62	15	83	0
42	24	63	15	84	1
43	23	64	14	85	0
44	24	65	12	86	1

TABLE V

COMPARISON BETWEEN THE THEORETICAL FREQUENCY DISTRIBUTION FOR FOUR FACTORS AND THE ACTUAL FREQUENCY DISTRIBUTION RESULTING WHEN CLASSES WITH A CERTAIN CONSTANTLY INCREASING RANGE ARE USED

Class limits	24–27	28–32	33–38	39–45	46–53	54–62	63–72	73–83	84–95
Class range.....	4	5	6	7	8	9	10	11	12
Frequency.....	6	27	94	183	210	189	94	23	2
Calculated frequency for 828 individuals for $(\frac{1}{2}+\frac{1}{2})^8$.....	3.2	25.9	90.6	181.1	264.4	181.1	90.6	25.9	3.2

however, if it calls attention to the manifest error of expressing a wide range of biological variation by a frequency polygon of equal size classes.

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Summary

Concluding, the following points may be again emphasized:

1. The inheritance of size complexes is so intricate that it is necessary to simplify an experiment upon them in every possible manner. The material used in this investigation, *Nicotiana forgetiana* Hort. Sand. and *N. alata grandiflora* Comes, lacks three of the complicating features that usually ensnarl such work. They are almost always naturally self-fertilized, and through numerous generations of self-fertilization have become automatically as homozygous in their characters as may be expected in plants that reproduce sexually. Their fecundity is so great that practically any quantity of F_2 individuals can be produced from a single F_1 plant. A plant character was investigated upon which the effect of environment is so small as to be negligible, namely corolla size.

2. These self-fertile species, which are perfectly fertile *inter se*, gave self-sterile progeny. This fact did not affect the production of an F_2 generation, as the F_1 plants from homozygous parents are alike in gametic constitution, and these were perfectly fertile *inter se*.

3. *N. forgetiana* with a mean corolla length of 25.6 mm. crossed with *N. alata grandiflora* with a mean corolla length of 78.8 mm. resulted in an intermediate F_1 generation with a mean variability of 44.3 mm.

4. The variability of the F_1 generation was very small, being about the same as that of the remarkably constant parental species. The F_2 generation, on the contrary, was very variable and both grandparental types were reproduced.

5. It is shown that the F_2 generation is what would be expected if the difference in corolla length shown by these two species were represented by the segregation and recombination of four cumulative but independent pairs of unit factors, dominance being absent.

6. The coincidence of theory and result is as great in this case as it is in qualitative characters of like complexity. If the Mendelian notation is useful to describe complex qualitative inheritance, it is similarly useful in describing the inheritance of quantitative characters.

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7. Length of style and of filament are perfectly correlated with corolla length.

8. Breadth of corolla shows an average correlation with length of corolla equal to 61 per cent.

9. The frequency distribution of corolla length for the F_2 generation is positively skew. It is pointed out that the range of fluctuations of corolla length in the two pure species is twice as great in the one of larger size than in the other. Classes of equal size in frequency distributions of great variability appear to be arbitrary and improper, if size factors are assumed to be dynamic factors with fluctuations roughly expressed by the term growth force. To show this accelerative action, the class ranges must gradually increase as the size (that is, the number of factors) increases. It is shown that the distribution under discussion will be changed from skew to normal if a simple arithmetical increase in the size of the classes is made.

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EXPLANATION OF PLATES

PLATE VI

At the left, a young flowering plant of *Nicotiana alata* Link and Otto, var. *grandiflora* Comes; at the right, a young flowering plant of *N. forgetiana* Hort. Sand.

PLATE VII

A mature plant of the first hybrid generation of a cross between *N. forgetiana* and *N. alata grandiflora*.

PLATE VIII

Figs. 1, 2, and 3, upper, median, and lower leaves of a mature plant of *N. alata grandiflora;* figs. 4, 5, and 6, upper, median, and lower leaves of the first generation of a cross between *N. forgetiana* and *N. alata grandiflora;* figs. 7, 8, and 9, upper, median, and lower leaves of a mature plant of *N. forgetiana*.

PLATE IX

At the left, a flower of *N. alata grandiflora;* at the right, a flower of *N. forgetiana;* between them are extreme F_2 segregates in length and spread of corolla; taken on the same plate, three-fourths natural size.

PLATE X

Fig. 1, *N. alata grandiflora;* fig. 2, *N. forgetiana;* fig. 3, cross between *N. forgetiana* and *N. alata grandiflora*, F_1 generation; the remaining figures are F_2 segregates; all figures are three-fourths natural size.

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THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. III

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH TWENTY-FIVE FIGURES)

The hydrarch successions

The bog succession

I. Physiographic development of the bog habitat

At the commencement of the glacial period the topography and the drainage system of what is now Isle Royale were very similar to those of today, except that lakes and swamps were few or absent. This topography was but slightly modified by the invasion of the ice, and the most important change effected by glacial erosion was the excavation of rock basins in the preglacial valleys. Since the retreat of the ice the gradual emergence of the island from the waters of the lake has taken place. In some cases inclosed basins appeared above the surface ready made; in others they were produced by wave-built bars thrown across the mouths of harbors or both ends of channels during pauses in the retreat of the waters. By continued emergence some of these rock basins and cut-off bays came to occupy positions far in the interior of the island. The tilting which followed the Lake Nipissing stage must have had some effect upon the island lakes thus formed. It may have brought about the partial draining of some, the enlargement and perhaps even origination of others, and occasional shifting of outlets; in all cases it must have produced a tendency toward migration to the southwest.

The physiographic development of the bog habitat thus includes as a rule two periods: first, the channel-bay stage, and second, the lake stage. Numerous localities that illustrate the process may be seen today, especially at the northeast end of the island. Duncan

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Bay would become a lake if the water level should sink 5–6 m.; Pickerel Cove is a similar case; and the inland portion of Rock Harbor is nearly closed at its narrowest point by a sand bar that has been built almost to the surface.

Several of the lakes of Isle Royale are of respectable size. Siskowit Lake, the largest, is more than 10 km. long and 2.5 km. wide (fig. 31). The majority are small, many being mere ponds.

All the lakes, and the harbors as well, are tending toward extinction through down-cutting of outlets, sedimentation, and vegetation. Down-cutting of outlets has as yet accomplished very

FIG. 31.—Siskowit Lake: the largest of the Isle Royale lakes

little. The large lakes like Siskowit are being filled by sedimentation with extreme slowness, because of the small size of the streams, their slight gradient, and the thick covering of vegetation which almost inhibits erosion of the land surfaces. It is impossible for bog vegetation to obtain a foothold in the large lake basins except here and there in very sheltered spots, because of vigorous wave and ice action (HOLT **33**, p. 218). They will therefore remain much as they are for a long time. In the small lakes, on the other hand, where wave and ice action are not severe, invasion by bog vegetation is in active progress.

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II. Vegetational development in the bog habitat

1. Channel-bay stage

Even as early as the channel-bay stage we find the beginnings of the vegetational history of the bog habitat. If the body of water be large or subject to considerable wave and current action, plant life is practically absent. In sheltered places, however, there lives a plant society, sparse but characteristic. The commonest species is *Isoetes macrospora* Dur. (quillwort), growing entirely submerged at a depth of 0.3–1 m. in the silty sediment that covers the bottom. *Isoetes* here attains an unusual size, the crowns being frequently 5 cm. and more in diameter. With it grow occasional plants of *Chara* (stonewort), *Ranunculus aquatilis* L. var. *capillaceus* DC (water crowfoot), *Potamogeton perfoliatus* L. and other spp. (pondweeds). On shoals and along the reefs at the ends of the narrow islands and points are frequent clumps of sedges: *Carex aquatilis* Wahlenb., *C. stricta* Lam., *C. lenticularis* Michx.

2. Lake stage

The lake stage is considered as extending from the first complete inclosure of the body of water to the time when the bog vegetation has brought about its extinction. During this physiographic stage all the vegetational stages of the bog succession usually appear in their accustomed order. The aquatics are already present and the sedge society has often made a slight beginning. The latter now develops with rapidity, especially in the smaller lakes, and is followed in turn by the sphagnum-shrub society and the bog forest.

a) Peat formation

Peat formation in the northern and southern peninsulas of Michigan has been described by TRANSEAU (56) and by DAVIS (19). The bogs which DAVIS studied, especially in the Upper Peninsula, are very similar to those of Isle Royale, and this author shows that the sedge mat is the most important agent in the formation of the peat. Lack of time and facilities prevented a study of the basin-filling process upon Isle Royale, but it is certain that the bulk of the peat is deposited through the formation and sinking of the sedge mat and the accumulation of finely divided material

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dropped from it. A subordinate amount is formed from the remains of the aquatic vegetation preceding the sedges in the invasion of the basins and from the shrub-sphagnum vegetation which follows them.

b) Illustrative localities

To illustrate the course of the bog succession upon Isle Royale several representative localities will be briefly described. Amygdaloid Lake shows the bog plants gaining their first foothold along the shore; the two ponds near Tobin's Harbor have been partially

FIG. 32.—Amygdaloid Lake: in the foreground a thick growth of *Menyanthes* and *Lysimachia thyrsiflora;* farther out, *Nymphaea advena.*

covered and filled; and the basin on Raspberry Island contains a completely covered bog.

Amygdaloid Lake (fig. 32).—Amygdaloid Island lies parallel to the northwest shore of Isle Royale and is formed by two partially submerged ridges of the usual kind. Between the ridges is an inclosed basin which contains a narrow lake, 100 m. wide at the most, but 1.2 km. long. It should be noted that Amygdaloid Lake is identically like the basin on Raspberry Island, to be described later, in situation and physiographic development. For some reason its history has not progressed so far, although both are at

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the present lake level. It may be that the basin has been more recently shut off from Lake Superior than that on Raspberry Island, and also the depression is larger and doubtless deeper. The climax forest descends to the edge of the interior lake, except for an occasional short strip of stony or sandy beach. At the southwest end there is a considerable amount of bog vegetation, growing in water a few centimeters deep and underlain by 2 m. of soft mud containing much organic material. The principal aquatic is *Nymphaea advena* Ait. (yellow pond lily). There is next a zone of amphibious plants dominated by *Menyanthes trifoliata* L. (buckbean), which is accompanied by *Lysimachia thyrsiflora* L. (bog loosestrife) and a few other species. As will be noted later, *Menyanthes* is frequently an important mat-former. Through the middle of this zone winds a narrow streamlike ribbon of water, probably the last remnant of a sluggish outlet. Back of the *Menyanthes* zone and filling the continuation of the basin for 0.5 km. is the bog forest, composed of *Larix* and *Picea mariana*, with *Alnus incana* (L.) Moench (hoary alder) in front.

The arrangement of the vegetation here illustrates a feature characteristic of the bog-filled depressions of Isle Royale. On account of the elongated form of the basins, the building out of the bog vegetation goes on much more rapidly at the ends of the lakes than along their sides, because of gentler slope. Theoretically, also, it should build out faster on the northwest side than on the southeast, since by reason of the rock structure the former slope is normally gentler than the latter. In a few cases notable difference was seen in the width of the sedge mat corresponding to the difference in slope, but usually the width of the zone on the two sides was about the same. Probably talus deposits, slope wash, and sediments of various kinds tend to lessen the slope of the southeast side, making it more or less equal to that of the other.

It has been stated that along the greater part of the lake shore the climax forest descends to the water's edge. At one point (a sandy stretch) bog vegetation was found to be obtaining its first foothold. Farthest out were scattering plants of *Nymphaea advena*. Close to shore grew scattered stools of *Carex filiformis* L. (bog sedge) and plants of *Eleocharis palustris* (L.) R. & S. (creeping

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spike-rush) and *Equisetum fluviatile* L. (scouring rush). Here we have the very beginning of the sedge mat, *Carex filiformis* being the most important mat-builder in most of the Isle Royale bogs. Next came a nearly bare level sandy shore 1–3 m. wide, at the upper edge of which began a second belt of bog vegetation. A line of depauperate *Menyanthes* with rootstocks creeping out over the gravel formed the lowest portion. It is probable that there has been a slight recent change of level in Amygdaloid Lake and that the *Menyanthes* marks the height of the former water surface. Above the *Menyanthes* was an area peopled by a number of species belonging partly to the bog forest and partly to the climax forest. These are as follows: *Lycopodium annotinum* L. (stiff club moss), *Smilacina trifolia* (L.) Desf. (three-leaved Solomon's seal), *Chiogenes hispidula* (L.) T. & G. (snowberry), *Symplocarpus foetidus* (L.) Nutt. (skunk cabbage), *Coptis trifolia* (L.) Salisb. (goldthread), *Linnaea borealis* L. var. *americana* (Forbes) Rehder (twin-flower), *Pyrola secunda* L. (shin leaf), *Cornus canadensis* L. (bunch-berry), *Trientalis americana* (Pers.) Pursh (star-flower), *Maianthemum canadense* Desf. (two-leaved Solomon's seal), *Mitella nuda* L. (mitrewort), *Moneses uniflora* (L.) Gray (one-flowered wintergreen).

This low vegetation was nearly smothered by a dense growth of sphagnum, much of it very young. The *Lycopodium*, which was the most abundant species of the list given above, showed only the tips of its branches except along the edge of the sphagnum mass, where thick clusters of new shoots projected from beneath the moss. The plants of *Coptis* were many of them buried up to the leaves. Upon the surface of the sphagnum grew *Drosera rotundifolia* L. (sundew) and *Linnaea*. A low beach ridge supported the most luxuriant sphagnum growth, which was occasionally as much as 0.3 m. deep, especially where it surrounded shrubs and tall grasses. *Calamagrostis canadensis* (Michx.) Beauv., *Agrostis hyemalis* (Walt.) BSP, *Iris versicolor* L., *Campanula uliginosa* Rydb. (bog bell-flower) grew here, and also *Alnus incana* (L.) Moench. (hoary alder). It is noteworthy that everywhere along the shore, except where the sphagnum has become established, *Alnus crispa* rather than *A. incana* forms the forest margin. In and around the sphagnum grew a few bog trees, *Larix* 1–3 m. in height, and young

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Picea mariana and *Thuja;* and back of these was a narrow band of bog forest, hardly more than a single line of large trees, *Larix* and *Thuja*, with much young *Abies* and *Betula*, and the usual herbaceous growth of such a habitat, practically the list given above. The sphagnum was evidently spreading from the ridge both toward the water and into this area of bog forest. Behind all was the climax forest of balsam, spruce, and birch.

It is evident from the foregoing description that at this locality we have in embryo every society or zone of the bog succession,

FIG. 33.—Sucker Lake: aquatics; sedge zone of *Carex filiformis* type, fringed with *Menyanthes;* at the left a narrow zone of shrubs and a thin line of tamaracks bordering the climax forest; a thick growth of bog trees at the end of the basin (distance).

from the aquatics through the sedge mat (represented by the stools of *Carex* and its companions), the sphagnum-shrub zone supporting the nascent bog forest, to the mature bog forest invaded by the climax trees; and all in the space of only 10 m. It is thus demonstrated that all the zones may begin their development at approximately the same time.

Sucker Lake (fig. 33; Sec. 34, T. 67 N., R. 33 W.).—The development of the bog vegetation is here far advanced. A wide zone of aquatics nearly surrounds the small area of open water, and this in turn is surrounded on three sides by a broad sedge mat made up of

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Carex filiformis L., *C. limosa* L., *C. chordorrhiza* L. f., *C. polygama* Schkuhr, *C. oligosperma* Michx., and *C. livida* (Wahlenb.) Willd. Along the outer edge of the mat and almost forming a zone by itself is a fringe of *Menyanthes*, its thick rootstocks closely intertwined. The shrub zone, dominantly *Myrica Gale* L. (sweet gale), is poorly developed, and sphagnum is nearly absent, only a sparse growth being seen and this nearly choked by the luxuriant sedges. Along much of the southeast shore the sedge mat is absent and the shrubs are the marginal vegetation. Here *Chamaedaphne* and

FIG. 34.—Pond near Tobin's Harbor in Sec. 5, T. 66 N., R. 33 W.: aquatics occupying center; sedge zone of *Carex filiformis* type; in the background hoary alder and tamaracks bordering the climax forest.

Andromeda grow actually in the water. DAVIS (19) has noted this replacement of the sedge zone by a shrub mat as a very common occurrence in the bogs of the northern peninsula of Michigan, but it is rare on Isle Royale. The bog forest at Sucker Lake is a mere line of tamaracks along the sides of the basin, but is well developed at both ends, where great stretches of the narrow depression have been converted into a forested valley. Sucker Lake is the last remnant of a body of water that was once very similar to the Rock Harbor of today.

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Pond near Tobin's Harbor (fig. 34; Sec. 5, T. 66 N., R. 33 W.).—This locality is closely similar to the last and occupies the same type of basin, with considerable bog forest at both ends. Development has proceeded one step farther, there being no open water, and the aquatics thus occupy the center. The sedge zone is continuous and everywhere equally developed. Soundings through the mat showed that the slopes of the bottom on the northwest and southeast sides are not notably different. *Carex filiformis* is the principal mat-former. The other species contributing are *Carex*

FIG. 35.—Same locality as fig. 34: *Scirpus hudsonianus* prominent in the sedge zone: islands of shrubs, *Alnus incana* surrounded by *Chamaedaphne;* a thick growth of bog trees at the end of the basin.

limosa L., *C. chordorrhiza* L. f., *C. Michauxiana* Boechl., *C. livida* (Wahlenb.) Willd., and *C. polygama* Schkuhr. The principal bog herbs accompanying the sedges are as follows: *Menyanthes trifoliata* L. (buckbean), *Potentilla palustris* (L.) Scop. (marsh cinquefoil), *Vaccinium Oxycoccos* L. var. *intermedium* Gray (cranberry), *Rhynchospora alba* (L.) Vahl (white beak-rush), *Cicuta bulbifera* L. (water hemlock), *Hypericum virginicum* L. (marsh St. Johnswort), *Scirpus hudsonianus* (Michx.) Fernald (alpine cotton-grass), *Epilobium palustre* L. (marsh willow-herb), *Scutellaria galericulata*

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L. (skull-cap), *Lysimachia terrestris* (L.) BSP (loosestrife), *Campanula uliginosa* Rydb. (bog bell-flower), *Galium Claytoni* Michx. (bedstraw), *Lycopus uniflorus* Michx. (bugle-weed), *Sarracenia purpurea* L. (pitcher-plant), *Drosera rotundifolia* L. (round-leaved sundew), *Iris versicolor* L., *Arethusa bulbosa* L., *Spiranthes Romanzoffiana* Cham. (lady's tresses), *Habenaria dilatata* (Pursh) Gray (white bog orchis), *H. psycodes* (L.) Sw. (purple-fringed orchis). *Sphagnum* is rare. The shrub zone is better developed than at Sucker Lake and includes two subzones: the outer, in which *Chamaedaphne calyculata* (L.) Moench is dominant and accompanied by *Andromeda glaucophylla* Link and *Salix pedicellaris* Pursh; the inner, of *Alnus incana* (L.) Moench. Advance islands of shrubs are scattered here and there over the sedge mat, the outermost being composed of *Chamaedaphne*, and the inner of a nucleus of *Alnus incana* surrounded by a circular zone of *Chamaedaphne* (fig. 35). Seedlings of tamarack are frequent in these colonies. The subzone of *Alnus incana* fringes the outer edge of the bog forest, which here as usual is a mere line along the sides, but broader at the ends. The bog tree is the tamarack.

3. Open bog stage: Raspberry Island bog

Raspberry Island is one of the row that bounds Rock Harbor on the southeast, and is next in line to Smithwick Island, studied in connection with the climax forest. Its upland forest cover was originally like that of Smithwick, but unfortunately this has been largely fire-swept, the bog area, however, having escaped unharmed. The island consists of two parallel ridges of the typical Isle Royale kind, bounding a narrow depression, closed at both ends by beach ridges, which contains the bog area. The outer ridge is the more massive of the two and makes the bulk of the island, while the inner is only half as long. Both reach an elevation of about 10 m. The island has emerged from the lake in comparatively recent time, and its history has been a simple one; moreover it is in all essentials the history of Isle Royale itself on a small scale. When the lake level was 3 m. higher than now there was a channel over the site of the bog area. At this time currents and waves were doubtless at work building bars across the channel mouths. With continued sub-

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sidence of the lake level the bar at the exposed southwest end emerged and became a beach connecting the two ridges, which now inclosed a sheltered bay. Into this considerable sediment was still being carried by waves and currents. As the lake level continued to fall, the more slowly building bar across the sheltered northeast end of the harbor emerged, and the bay was now an inland lake. It is probable that the height of both beaches has been increased since their emergence through the agency of storm waves. The physiographic history of the habitat is thus concluded. Its likeness to Amygdaloid Island will be at once evident. At Amygdaloid Lake we find the beginnings of the bog vegetation; Raspberry Island shows its culmination, in the sense that at this stage the open water has disappeared, and all the bog societies are present and at their best development. The further history will record the progressive extinction of these societies by centripetal invasion.

The relations of the zones to each other are shown in the

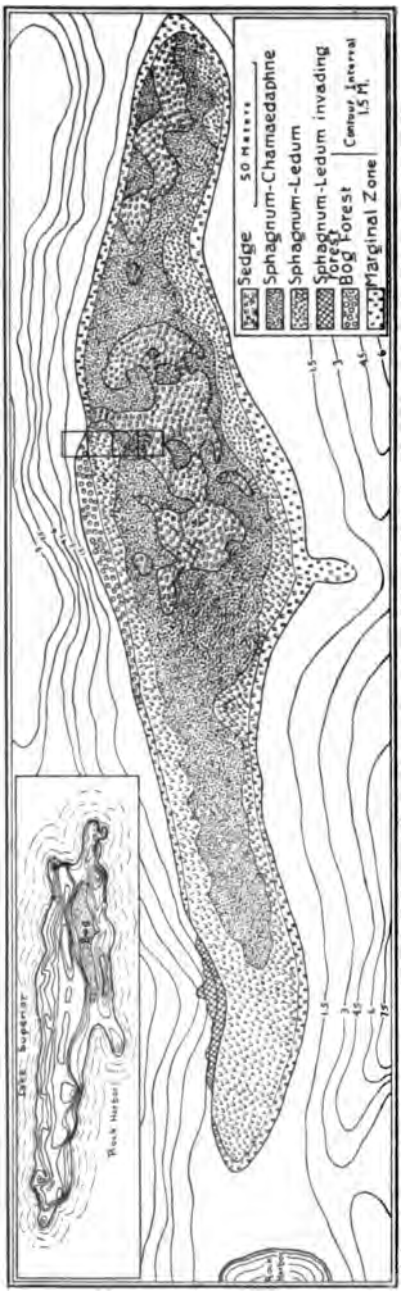

FIG. 36.—Map of Raspberry Island (upper left-hand corner) and the bog area on a larger scale: the location of quadrat 9 is shown

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map (fig. 36) and in the general view (fig. 37). Certain features of the succession were so well developed in this bog that they must have a place in this account.

The sedge mat is composed almost entirely of *Carex limosa* L. (mud sedge) (fig. 38). Occasional bare muddy spots are nearly free of sedge, but support a scattered growth of *Menyanthes* and *Drosera anglica* Huds. (narrow-leaved sundew). These appear to represent the youngest stage now existing in this habitat.

FIG. 37.—Raspberry Island bog: general view; sedge zone of *Carex limosa* type in the foreground; the sphagnum-shrub society occupies most of the view; young bog trees as pioneers of the forest; black spruce prominent in the bog forest.

a) The sphagnum and its relations

Particular attention was given to the sphagnum, which is very luxuriant in this bog; especially to its point of origin, the conditions governing its spread, and its relations to companion species.

The first point to be noted is that the sphagnum is a superficial layer supported upon the sedge mat, and thus does not contribute in any large degree to peat formation. This feature has been noted by HOLT (33) for the Isle Royale bogs, and by TRANSEAU (56) and DAVIS (19) for the northern and southern peninsulas of Michigan.

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The next important fact is that the sphagnum does not make its first growth at the extreme edge of the bog area and from here works its way centerward only. On the contrary, it begins its growth some distance within the bog margin and works both ways; very slowly toward the margin, faster toward the center. Proof of this course of events is seen in the entire absence of sphagnum from the marginal zone, except in certain parts where it is manifestly a recent invader. Soil samples taken at various depths in

FIG. 38.—Sedge zone of *Carex limosa* type; Raspberry Island

the marginal zone, examined microscopically, failed to show the slightest trace of sphagnum remains, although these are long preserved and readily recognized. Another proof is found in the form of the sphagnum accumulation, which is that of a ridge parallel to the bog margin and at a somewhat constant distance from it. This ridge usually has its greatest thickness close to the outer (marginal) side, doubtless marking here the region of first growth. It will be remembered too that in the primitive stage observed at Amygdaloid Lake the sphagnum was seen to be spreading both ways. The face toward the bog margin (on Raspberry Island) is usually rather abrupt, forming a prominent wall which bounds the marginal zone. Occasionally a thin layer of sphagnum is found

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to be invading the latter area. In the opposite direction (centerward) the sphagnum decreases *gradually* in thickness, and at its edge invasion of the sedge zone is actively taking place. Fig. 39, drawn to scale, is a typical bog section. The form of the ridge is shown and also the depth at various points. The high projection upon the sphagnum mass is a hummock, the true marginal face being at the right. A tongue of the moss is seen invading the marginal zone. Below the line which is drawn as marking the base of the sphagnum the soil is black peat containing little that is recognizable even with a microscope. At several places, however, sphagnum fragments were recognized in various degrees of abundance some centimeters below the line indicated. These were

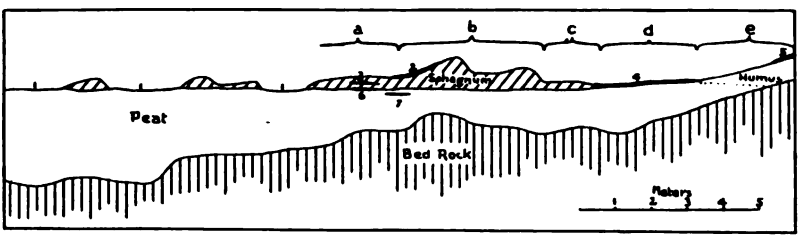

FIG. 39.—Section through Raspberry Island bog: *a*, *Sphagnum-Chamaedaphne; b*, *Sphagnum-Ledum; c*, *Sphagnum* invading marginal trench; *d*, marginal trench; *e*, upland; *1*, sedge zone; *2*, *Calliergon Schreberi; 3*, *Calliergon Schreberi* (fossils); *4*, *Carex trisperma* and *Hylocomium proliferum; 5*, *Hylocomium proliferum; 6*, *7*, *Drepanocladus vernicosus* (?) (fossils).

probably washed down from above, since this line certainly indicates the plane at which the growth began.

The development of the sphagnum has not made uninterrupted progress, for at *3* on the section a stratum was found which contained abundant fragments of *Calliergon Schreberi*, and at *6* and *7* remains of *Drepanocladus vernicosus* (Lindb.) Warnst. were discovered. These two species evidently obtained a foothold upon the surface of the sphagnum and for a time arrested its growth over certain areas. The latter again gained the upper hand and buried the invaders.

The zone included between the sphagnum and the slopes of the upland commonly takes the form of a circular trench. This "marginal trench" is a widespread feature of bogs, and various

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causes for its occurrence have been suggested by MacMillan (38), Shaw (52), Davis (19), and Atkinson (5). None of these explanations could be applied with certainty to the phenomenon as observed upon Isle Royale, but that offered by Atkinson seemed most plausible, that is, that during the early development of the sedge mat the sphagnum was excluded by the shade cast by the near-by forest growth. Only after the bog substratum had built out beyond the shaded area did the moss become established upon it.

Fig. 40.—Tension zone between sedge and sphagnum-shrub societies: *Carex limosa* and *Chamaedaphne* keep pace with the growth of the sphagnum by upward elongation; Raspberry Island.

The third point to be considered is the manner of invasion by the sphagnum, including its relations to the sedges and other plants which it finally replaces, and to the shrubs which accompany or follow it. The sphagnum area spreads marginally, and at the same time colonies of young plants originate among the sedges in advance of the main mass. Several such colonies are shown on the map (fig. 36). By the coalescence of these and the solid mass behind, the sphagnum zone extends itself at the expense of the sedge mat.

Certain plants of the sedge zone persist for some time after the sphagnum has gained control. They do this by a process of upward

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elongation, keeping pace in this way with the building up of the moss. *Carex limosa* itself survives for a considerable time. Stalks of this species apparently growing on the sphagnum can always be traced down to the stratum beneath, and the buried portions are found to be covered with dead remnants of leaves (fig. 40). *Menyanthes* manages to persist for a time in a similar way. *Sarracenia*, which as a rule precedes the sphagnum, makes use of the same method in an endeavor to hold its own, but is less successful

FIG. 41.—Zonal arrangement of bog shrubs: *Andromeda* in the foreground, mainly upon the sedge mat; *Chamaedaphne* (middle ground at the right) mainly upon a mound of sphagnum; Raspberry Island.

and is soon buried. Certain of the bog shrubs belong to the same class. *Chamaedaphne*, *Andromeda*, and *Salix pedicellaris* usually precede the sphagnum. When the moss starts its growth in the vicinity of these plants it builds up rapidly around their stems, forming the hummocks that are so characteristic of sphagnum bogs. Of the three shrubs, *Chamaedaphne* has the greatest power of holding its own against the smothering tendency of the moss (fig. 40); the willow is next; while *Andromeda* soon succumbs.

The two important bog shrubs, *Andromeda* and *Chamaedaphne*, are zonally arranged (fig. 41). *Andromeda* grows freely on the sedge mat, especially in the wetter parts, is most abundant just at the

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edge of the sphagnum, and occurs to a limited extent some distance back in the moss. *Chamaedaphne* is also found commonly upon the sedge mat, but inhabits the drier portions. In the sphagnum area it is abundant and over a wide belt almost the only shrub, extending back until it meets the zone where *Ledum groenlandicum* is the dominant species. Relative ability to withstand extreme wet bog soil conditions determines this zonation at the beginning, but the sudden elimination of *Andromeda*, leaving *Chamaedaphne* in full control, is due principally to the smothering effect of the sphagnum, which the former shrub is unable to avoid. *Chamaedaphne*, on the other hand, is able to grow up with the moss indefinitely, and therefore persists until the entrance of *Ledum* introduces a new factor. It is not certain that *Chamaedaphne* does not sometimes germinate upon the surface of the sphagnum as well as upon the sedge mat, and thus in part maintain its dominance. It is certain, however, that *Andromeda* does not commonly do so, at least not successfully. Two other shrubs, *Kalmia polifolia* Wang (pale laurel) and *Betula pumila* L. (dwarf birch), occur in this and other bogs, but not in sufficient abundance for satisfactory study of their habits.

Upon the surface of the sphagnum another group of species becomes established. Important among these are *Carex pauciflora* Lightf., *Smilacina trifolia* (L.) Desf. (three-leaved Solomon's seal), *Drosera rotundifolia* L. (round-leaved sundew), *Vaccinium Oxycoccos* L. (small cranberry). All of these are able in greater or less degree to keep pace with the continued upward growth of the moss.

Of far greater importance than these is *Ledum groenlandicum* Oeder (Labrador tea), which becomes established long after the other shrubs, indeed after all but *Chamaedaphne*, have disappeared. *Ledum* is almost invariably found to be related definitely to the sphagnum, its whole root system being contained within the mass. The growth that it forms is very dense (fig. 42), and as it is a taller shrub than *Chamaedaphne* it shades it severely, and thus finally causes its elimination. Its effect upon the sphagnum is similar. Because of the shade which *Ledum* produces and the considerable amount of waste which falls from it, the upward growth of the moss is gradually retarded and finally ceases altogether.

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About this time or often before, young plants of other mosses more or less tolerant of shade become established upon the higher parts of the sphagnum mass. *Polytrichum strictum* Banks is the first arrival, and *Aulacomnium palustre* (L.) Schwaegr. and *Calliergon Schreberi* (Willd.) Grout soon follow. These species form mats of continually increasing lateral extent, which put an effectual stop to further upward growth of sphagnum.

FIG. 42.—*Sphagnum-Ledum* zone, the moss entirely concealed by the abundant growth of the latter; the edge of the bog forest in the background; Raspberry Island.

b) Sphagnum invading the forest

The fact has been mentioned that the sphagnum frequently spreads into the marginal zone as well as toward the center of the bog. In some places this invasion is so effective that the marginal zone is entirely obliterated. The moss does not always stop even here, but occasionally climbs entirely out of the bog, invading the climax forest. A case of this kind was reported by HOLT (**33**) from a locality near Siskowit Lake. A far more striking instance was discovered on Raspberry Island, near the northeast end of the bog (see map, fig. 36 and fig. 43). In a stretch of 50 m. along the margin the sphagnum had completely obliterated the marginal zone and had ascended the slope for varying distances. At the point of

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farthest advance the mass had taken the form of a tongue 4 m. wide, extending 10 m. from the true bog margin. The slope of its surface was about 25° and the highest point reached was 4.5 m. above the bog level. The sphagnum supported a luxuriant growth of *Ledum* which completely covered it. The unusual abundance of flowers in comparison with the plants of the bog itself was a noteworthy feature, as was also the comparatively small size of the leaves, both facts perhaps indicating somewhat hard conditions. *Vaccinium Oxycoccos* and *Chiogenes hispidula* were also abundant, and frequent small seedlings of birch, black spruce, and balsam were found. The depth of the moss was 0.6–1 m., and the edges were abrupt, but unfortunately the fire which destroyed the upland forest had encroached somewhat upon the bog vegetation, so that the marginal conditions could not be ascertained.

FIG. 43.—*Sphagnum-Ledum* society invading the upland forest: the view is taken from the bog, and shows the bog vegetation climbing the slope to a height of 4.5 m.; Raspberry Island.

4. The bog forest and its development

Although in the Raspberry Island locality the bog forest is not so extensively developed as in other places, all the essential features are present. A series of four adjoining units was laid out, each 5 m. square, the whole forming a broad section cutting through all the societies from the sedge zone to the climax forest (quadrat 9, fig. 44). The manner of invasion of the sedge mat by the sphagnum is shown. To avoid confusion the distribution of the bog shrubs is indicated only in a general way. The trees of the various species, their locations, and ages are given in the manner made use

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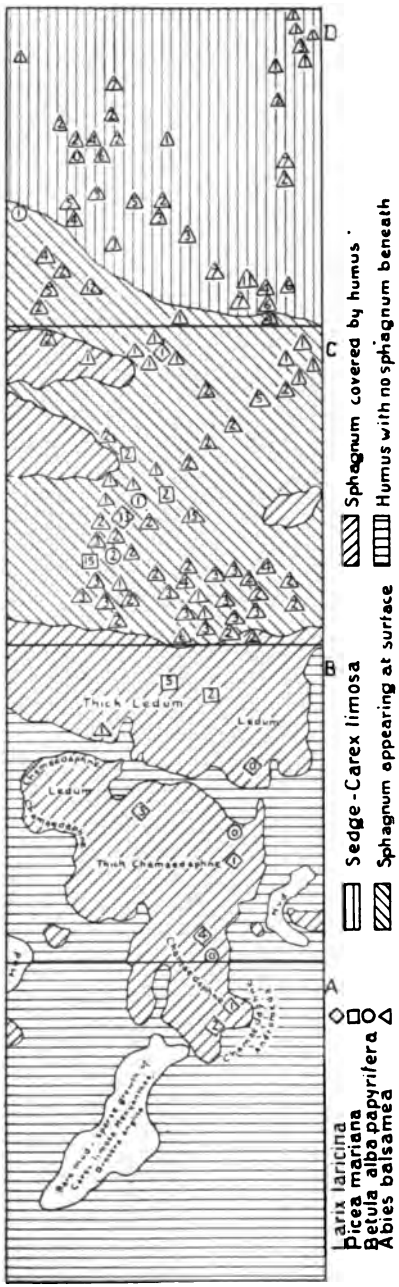

FIG. 44.—Quadrat 9: Raspberry Island; for explanation of symbols see fig. 6

of in the charts of the climax forest.

The most important fact to be obtained from the diagram is that in no part of the section is there anything approaching pure bog forest. In quadrats *A* and *B* there is a mere scattering of invaders; *C* and *D* are occupied by a young climax forest growth with a few bog trees, most of which are relicts. The absence of pure bog forest is due to the fact that the trees of the climax stage follow immediately after the first invading bog trees, or even accompany them. In accordance with the usual habit of the species, balsam seedlings germinate in enormous numbers, and although many of them succumb to the stress of competition, they shade the ground so that no more bog trees, which are light-requiring species, can start. The climax trees, *Abies*, *Betula*, and *Picea canadensis*, having come into possession are able to hold their ground in the manner described in an earlier section of this paper. The further history merely records the gradual dying out of the bog relicts.

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Though there is little *pure* bog forest upon Isle Royale, there is abundance of a very characteristic type which may be called "impure" bog forest; that is, forest composed of a mixture of bog and climax trees. Upon Raspberry Island it is poorly developed,

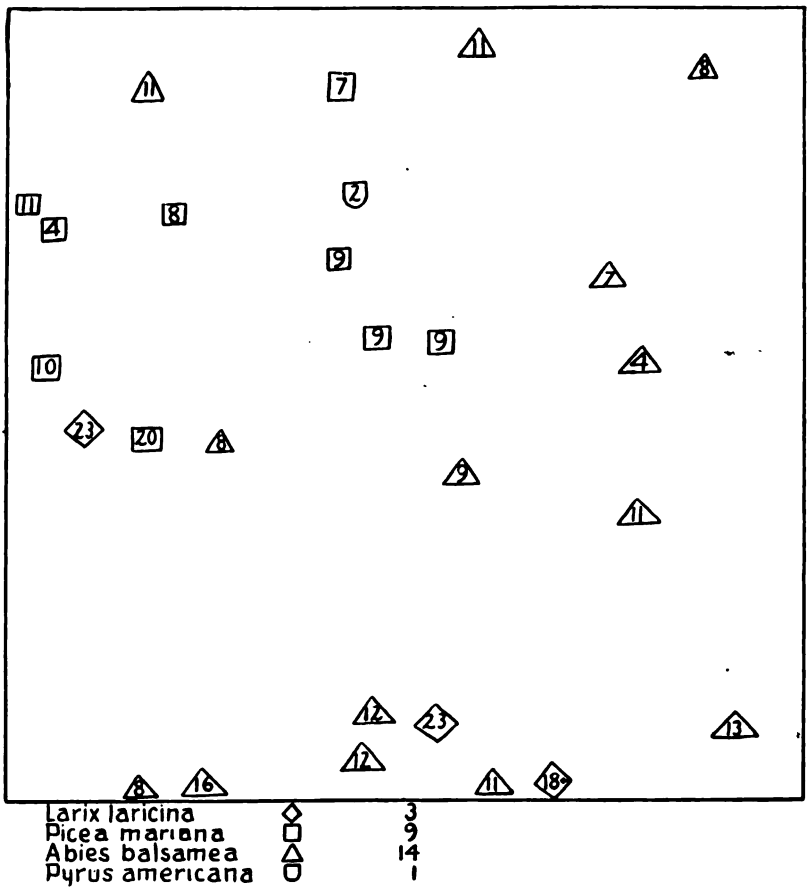

FIG. 45.—Quadrat 10: bog near Park Place Hotel; for explanation of symbols see fig. 6.

but there is an excellent sample near the Park Place Hotel on Rock Harbor (Sec. 3, T. 66 N., R. 33 W.). A quadrat in this locality was studied and the results are shown in fig. 45. The oldest trees here were the three tamaracks, and they were also much the largest, being 2.75–5.25 dm. thick, and towering above their companions.

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One of them was hollow, and all were more or less attacked by rot. The black spruces were found to be somewhat younger than the tamaracks. All were solid to the heart. The balsams, which were most numerous of the tree species, were of various ages from 47 to 161 years. No young balsams were present and the average age was very high (105 years). All showed signs of suppression during early life, probably due to shading by the faster growing bog trees. Within the last half-century the tops have reached the sunlight, and most of the balsams are now growing rapidly, though many are rotten hearted, as is common with this species. Two birches close to the quadrat, 1.5 dm. and 2.25 dm. in diameter, were found to be 62 and 69 years old respectively. No white spruce occurred in this locality, but the species is present in most areas of bog forest. A striking fact is the absence of reproduction (fig. 46). No tree younger than 47 years was seen except a few one or two-year-old seedlings of birch and mountain ash, which seem able to germinate in deep shade but not to continue growth.

FIG. 46.—Bog forest interior; locality of quadrat 10: two large tamaracks in the background; black spruce, balsam, and *Alnus incana;* carpet of *Carex trisperma* with *Petasites* and other species; note absence of tree reproduction.

The history of the area is probably as follows. The present generation of trees of both bog and climax type started during the period of open bog conditions, and growing up together produced so dense a shade as to inhibit the starting of new growth beneath them. Shelter from wind, due to the depression in which they grow, is doubtless the reason for the absence of windfalls and the unusually long life of the balsams. No reproduction will take

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place until light is admitted to the forest floor by the destruction of some of the present generation.

The characteristic bog forest shrubs are the alders. *Alnus incana* is found principally near the bogward edge, while *Alnus crispa*, belonging rather to the climax forest, inhabits the landward portions.

In the lower vegetation mosses are most prominent both in quantity and variety; 22 species were taken from a single area of bog forest. *Sphagnum* spp. (relicts of the open bog stage), *Calliergon Schreberi* (Willd.) Grout, and *Hylocomium proliferum* (L.) Lindb. make up the bulk of the moss carpet. Sharing the forest floor with these is *Carex trisperma* Dewey which, accompanied by *C. leptalea* Wahlenb. and *C. tenella* Schkuhr, forms dense green mats of considerable size. In some places *Lycopodium annotinum* L. covers the ground, and in others there is a rank growth of *Equisetum sylvaticum* L. As minor features there are certain herbs that particularly characterize the bog forest. The most numerous are *Habenaria obtusata* (Pursh) Richards, *Listera cordata* (L.) R. Br., *Smilacina trifolia* (L.) Desf., *Phegopteris Dryopteris* (L.) Fée, *Mitella nuda* L., *Coptis trifolia* (L.) Salisb., *Viola incognita* Brainerd, *Petasites palmatus* (Ait.) Gray.

The outstanding feature in the later part of the bog succession is the telescoping of stages. The sphagnum-shrub stage (when present) is hardly well established before the bog trees enter, and immediately following them or often actually with them come the climax trees. The reason for the early establishment of the latter is found in the likeness between the bog soils and those of the forested uplands. Those of the uplands are nearly as peaty in texture and properties as are those of the bogs. The causes of the peatiness of the upland soils trace back to other factors: low evaporation rate due to low temperatures; poor drainage because of solid rock substratum; and probable paucity of certain types of bacterial and fungal life. It follows, the two soils being much alike, that whatever trees can grow upon one may exist also upon the other.

5. Two types of bogs

One of the numerous questions that could not be settled with entire satisfaction related to two fairly distinct types of bogs

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involving somewhat different courses of succession. One had an abundant growth of sphagnum associated with much *Ledum*, and *Picea mariana* and *Larix* composing the bog forest. Those of the other type had little sphagnum, often practically none, and in these *Ledum* was rare or absent and *Picea mariana* almost never found, the bog trees being *Larix* and *Thuja* or *Larix* alone. The Raspberry Island bog is an excellent example of the first, which we may designate the sphagnum type; and Sucker Lake and the other pond near Tobin's Harbor illustrate the second, or sedge type. In some cases these types may represent stages in the same succession, since sphagnum often does not become dominant until late in the history of a bog, and *Ledum* and *Picea mariana* follow the sphagnum, being dependent upon its presence. But it is certain that in many cases the *Sphagnum-Ledum* stage is entirely eliminated, and that when this happens *Picea mariana* does not appear, or holds a very subordinate place in the bog forest. The succession in such cases is as follows: (1) aquatics, (2) sedge mat, (3) shrub zone (*Chamaedaphne*, *Andromeda*, *Alnus incana*), (4) bog forest (*Larix*, often with *Thuja*). It is obvious that *Sphagnum* is the critical plant, since *Ledum* and *Picea mariana* come later and only in bogs where the moss is abundant.

Certain differences were noted in the conditions prevailing in the two types of bogs. It was universally true in the sphagnum bogs that were visited that the drainage was poor or lacking, the only water loss being due to very slow seepage and evaporation. Those of the sedge type on the contrary were usually well drained. There was often open water in the center, in which case the bog might well be at a stage earlier than that of sphagnum dominance. The covered bogs without much sphagnum usually possessed one or more small streams flowing in and an active outlet. In a few cases, however, the drainage was seemingly as poor as in the sphagnum bogs. As to the way in which these drainage differences affect the vegetation, if they do affect it, nothing was determined.

Another fact was noted which quite certainly has a bearing upon the presence or absence of sphagnum. It was found that the sedge mat is composed of different species in the two types of bogs. In the sphagnum bogs *Carex limosa*, a low, soft, loosely growing

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stoloniferous species, was usually the principal mat-former, and *Menyanthes*, with somewhat similar characteristics, was next in importance (compare figs. 33 and 38). In those of the sedge type, tall stiff sedges growing in dense clumps were most important, forming a thick meadow-like growth. *Carex filiformis* was the commonest species, but certain areas were found to be dominated by *Scirpus caespitosus* L., the most densely tufted of all the sedges. These two kinds of sedge mat form very different substrata for the growth of the sphagnum. On account of the shortness and softness of *Carex limosa* the moss is never seriously shaded where that sedge is dominant, and it is able to grow over and around the *Carex* and *Menyanthes* plants and thus to spread laterally with ease. The sedges in this case offer no effective resistance, and the sphagnum soon gains the ascendancy over them. Where *Carex filiformis* and plants of similar habit are the principal mat-formers the moss, if it starts among the closely placed clumps, is shaded from the beginning. It cannot spread laterally among the dense clusters of thick culms, and so remains in a half-smothered condition until exterminated through the advance of the shrubs and trees. The distribution of the two kinds of mat-forming plants still remains to be accounted for, and for this I have as yet no explanation. It is entirely possible that the type of sedge which gains the dominant place in a given bog may be determined merely by accidental causes.

FIG. 47.—Bog forest in well drained portion of a bog near Siskowit Lake: *Larix* and *Alnus incana*.

Occasionally the two phases may be seen in a single bog. For

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instance, in a locality near Siskowit Lake (Sec. 32, T. 65 N., R. 35 W.) the central area (which is better drained than the rest, having a sluggish stream meandering through it) is of the sedge type. Some patches of bog forest near the stream are made up almost entirely of *Larix*, with much *Alnus incana* as undergrowth. In the poorly drained areas near the margin the forest is pure *Picea mariana*, and the ground is carpeted with solid sphagnum covered with an abundant growth of *Ledum*. These two phases are shown in figs. 47 and 48.

FIG. 48.—Bog forest in poorly drained area; same locality as fig. 47; *Picea mariana*, *Ledum*, and *Sphagnum*.

The delta swamp succession

I. Extent and distribution

The delta swamp succession comprises the successive stages of vegetational development which culminate in the establishment of the climax forest upon the deltas and alluvial plains of the streams. These societies do not occupy an extensive area in the aggregate, but they are exceedingly interesting because of the close interdependence between the successional and the physiographic processes. Delta swamps of various sizes are found at the heads of most of the bays, and are probably present also where streams of any size enter the larger lakes. Protection from the waves and currents of Lake Superior is naturally essential to their development. The localities studied were as follows: head of McCargoe's Cove (Sec. 26, T. 66 N., R. 35 W.), Brady Cove (Sec. 18, T. 66 N., R. 35 W.), Duncan Bay (Sec. 6, T. 66 N., R. 33 W.), Lake Richie outlet at Chippewa Harbor (Sec. 18, T. 65 N., R. 34 W.), Hay Bay (Sec.

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24, T. 64 N., R. 37 W.), head of Siskowit Bay (Sec. 33, T. 64 N., R. 37 W.).

II. Physiographic development of the habitat

The history of the present deltas began with the initiation of stream activity as the island emerged from the lake. The amount of erosion accomplished by the streams of Isle Royale has been very slight. The sources of the materials transported by them have been principally two: the products of wave erosion left high and dry as the lake level sank, and weathered rock material, including some decomposed by organic agencies. Deposits were made at the mouths of the streams at all stages during the emergence of the island. As the lake surface sank these were transported to successively lower levels, and more materials were added. Of course some of the earlier deposits may have been so situated as to have escaped removal, but no such remnants have been reported. It is therefore probable that the present deltas include most of the materials that made up the earlier ones, brought down from level to level as the streams were repeatedly rejuvenated by successive sinkings of the lake surface.

Delta building seems to have practically ceased, at least temporarily, for three reasons: (1) the available loose material accumulated during the successive stages has all been brought down and deposited; (2) the complete forest covering of the uplands practically inhibits further weathering and erosion, except what may be accomplished by the slow organic processes; (3) (applicable only to northeastward-flowing streams, which, however, are in the majority) tilting has taken place in the Lake Superior region since the formation of the Nipissing beach (ADAMS 4). At Isle Royale the elevation of this beach is about 18 m., and it rises northward to 27 m. at Nipigon. This has decreased the gradient of northeastward-flowing streams and thus has tended to reduce their erosive and transporting power.

The result of these processes has been the formation of flat delta plains of gravel, sand, and silt at the heads of many of the harbors, with streams, practically currentless, meandering over them. Cut-and-fill and scour-and-fill are going on to some extent

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in these streams, which processes are due principally to alternating currents produced by seiche movements (ADAMS 4) of the waters of Lake Superior. The currents thus produced are quite considerable. At one moment there is a strong outward flow; a few minutes later the movement may be just as swift in the opposite direction. The effect of the seiche current is practically the same as that of an ordinary stream current. It undermines the bank in some places and deposits the eroded materials in others. On account of its alternating direction the gradational effects in a particular case cannot be so simply worked out, but judging from the relative positions of the eroding and depositing portions of the banks it seems probable, as one would naturally expect, that the outward current is the more effective. It is possible that occasional heavy rains may considerably increase the volume and velocity of the streams. The channels are not ordinarily sunk far into the sedimentary substratum. Their banks appear largely as vertical sections of the layer of plant growth which has spread over the delta plain.

III. Vegetational development in the habitat

The first vegetation upon the delta deposits enters when the water over them shallows sufficiently to permit the growth of aquatics of the pondweed type. Next come water lilies and rushes, and when the sediments accumulate until they reach nearly to the surface, sedges gain a foothold and soon form a mat. Up to this point the development has followed the same course as the bog succession. Important differences now appear. The sedge mat does not build out over the water, probably because of wave and ice action, since the bodies of water into which the streams flow are rather large and open. The sedge mat stage does not last long, but is very soon superseded by a dense growth of tall grasses, among which *Calamagrostis canadensis* (Michx.) Beauv. is by far the most important. It is this type of plant, growing in dense, closely placed stools, that forms the bulk of the stratum of plant remains which finally covers the plain. The grasses are followed by shrubs, and these by the swamp trees, which finally give way to the climax forest.

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Among the delta swamps studied, the largest was at the head of McCargoe's Cove. The alluvial flat was here 0.8 km. long by 0.4 km. wide. All the stages are here well developed except the swamp forest, which has been fire-swept. Part of the meadow-like marsh is shown in fig. 49, and a sketch map of the delta is given in fig. 50. Farthest out, in water a meter and more deep, is a zone of *Potamogeton perfoliatus* L. Within this, in a few inches of water, grows *Equisetum fluviatile* L. Next comes the sedge mat, firmly grounded, with *Carex filiformis* as the principal species, accompanied

FIG. 49.—Delta swamp at the head of McCargoe's Cove: sedge, grass, and shrub societies are shown; the swamp forest has been burned.

by bog herbs. The area dominated by *Calamagrostis* is the most extensive, and its level is perceptibly higher than that of the sedge zone. With *Calamagrostis* grow other herbaceous species, many of them tall, such as *Thalictrum dasycarpum* Fisch. and Lall. (tall meadow rue), *Chelone glabra* L. (turtle-head), *Epilobium angustifolium* L. (fireweed), and *Symplocarpus foetidus* (L.) Nutt. (skunk cabbage). Stools and patches of *Calamagrostis* were seen as invaders of the sedge society, and occasional shrubs, pioneers of the next group, were scattered over the area occupied by the grass.

Myrica Gale L. (sweet gale) is the first shrub to invade the

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meadow swamp. It is followed by *Alnus incana*, which at first is pure, but farther back is found mixed with other shrubs: *Cornus stolonifera* Michx. (red osier dogwood) and *Viburnum pauciflorum* Raf. (high bush cranberry). With these come the invaders from the forest, *Fraxinus nigra* Marsh (black ash) being usually the first arrival. Burned stumps indicate that there was once an extensive development of swamp forest along the east side of the delta, in which *Thuja* was the important tree.

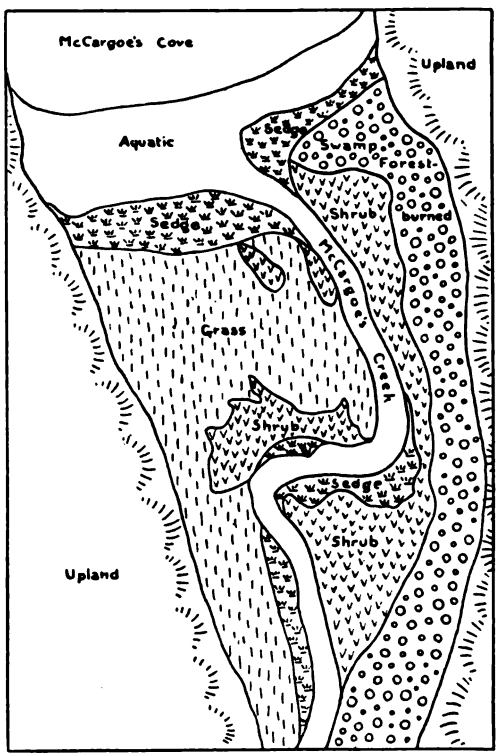

FIG. 50.—Sketch map of the delta at the head of McCargoe's Cove.

The stream which winds through the swamp is 6–10 m. wide and 0.3–1 m. deep. Its channel is constantly changing by reason of its own undermining and depositional activity. Near the outer edge of the marsh it crosses the belt of sedges. Farther back it is bordered by various societies. Where it cuts into the grass-covered areas erosion by undermining is going on, and a section of peat sometimes 0.6 m. in height is exposed. For considerable distances shrubs are also being undermined, and at one point the stream in its meandering has invaded the area of former swamp forest and has caused the overthrow of many trees. The material eroded from the banks is deposited where the current slackens, and in such places the normal succession of plant stages is in progress; aquatics first, followed by a sedge mat when the

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deposit reaches the surface. Frequently the first invaders are stools of sedge or rootstocks of *Nymphaea* and *Calla* which have been washed out from some eroding portion of the shore.

It may thus be seen how the plant life supplements the physiographic processes. Upon one bank the current may be steadily destroying the vegetation (grasses, shrubs, and even trees); while on the other, where deposition is in progress, the same types are being developed through the normal course of the swamp succession.

Note should be made of the peculiarly rich aquatic flora which inhabits the shallows of this and similar sluggish streams. The list of species obtained in the several localities of this type includes the following of special interest: *Nymphaea advena* Ait., *Vallisneria spiralis* L., *Utricularia vulgaris* L. var. *americana* Gray, *U. intermedia* Hayne, *U. minor* L., *Myriophyllum verticillatum* L. var. *pectinatum* Wallr., *M. spicatum* L., *M. alterniflorum* DC, *Potamogeton natans* L., *P. alpinus* Balbis, *P. amplifolius* Tuckerm., *P. heterophyllus* Schreb., *P. heterophyllus* f. *terrestris* Schlecht., *P. praelongus* Wulf., *P. perfoliatus* L., *P. zosterifolius* Schumacher, *P. obtusifolius* Mertens and Koch, *P. filiformis* Pers., *Callitriche palustris* L., *Castalia tetragona* (Georgi) Lawson, *Bidens Beckii* Torr., *Scirpus subterminalis* Torr., *Sparganium diversifolium* Graebner, *S. minimum* Fries, *Sagittaria latifolia* Willd. f. *hastata* (Pursh) Robinson, *S. cuneata* Sheldon, *Lemna trisulca* L., *Ceratophyllum demersum* L., *Hippuris vulgaris* L., *Glyceria borealis* (Nash) Batchelder, *Calla palustris* L., *Isoetes macrospora* Dur. Though not a plant, *Spongilla* should be mentioned as an important element in the aquatic life.

At the head of Duncan Bay there are two delta swamps, both smaller than the one just described. One of these was studied with care, and the locality is included here because the swamp forest is well developed. *Fraxinus nigra* is the pioneer, and is present, but not abundant, in the mature forest. *Thuja* comes next and is the most important species. *Larix*, *Picea canadensis*, *Abies*, and *Betula alba* var. *papyrifera*, in order of abundance as named, complete the list. In passing toward the shoreward edge of the swamp forest *Larix* is the first to disappear. *Thuja* holds out much longer, and the ground is covered in places with tangles of layered branches

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from it. The young trees are largely balsams. The herbaceous growth is practically the same that is found in the bog forest. It will be noted that all the trees of the climax forest are present here, and that the stages are telescoped as in the bog succession.

A locality where the climax condition had been almost attained was found in a narrow stream valley at the head of Brady Cove (Sec. 18, T. 66. N., R. 35 W.). The forest here, which fills the valley, is of the climax type except for an occasional ancient *Thuja* and a slight admixture of *Fraxinus nigra*. Fallen trunks of *Thuja* are fairly numerous. The shrubs and herbs are a mixture of swamp forest and climax forest species.

That there is a general resemblance between the bog succession and the delta swamp succession is very evident. There are also some striking differences which are constant in the localities studied. Most important of these are the following: sedge mat not floating; interpolation of grass stage as the most important peat-forming agency; absence of sphagnum, true bog shrubs, and *Picea mariana;* dominance of *Thuja* in the swamp forest.

It is conceivable that under certain circumstances one succession might pass over into the other. This seems to have happened at the head of Siskowit Bay just north of Senter Point. A large swampy area has been cut off from the bay by a high curving beach ridge 1 km. long. That there was originally a delta swamp here is shown by the presence of a remnant of the former stream, a winding strip of water ending abruptly against the outer ridge. For some reason, possibly on account of post-Nipissing tilting, the current of the stream became insufficient to keep its outlet open in opposition to the vigorous wave action upon the shore of the bay. The resulting stagnancy has brought about a partial change to bog conditions. The former stream is partly filled with an open growth of *Menyanthes*, *Equisetum fluviatile*, *Utricularia intermedia*, and *Potamogeton heterophyllus*. Along the water's edge there is a band of nearly pure *Carex filiformis*, recently established. The body of the swamp is occupied by a sedge-grass society, in which *Scirpus caespitosus* is dominant. Accompanying species are *Carex exilis* Dewey, *Muhlenbergia racemosa* (Michx.) BSP, *Sarracenia purpurea* L., *Vaccinium Oxycoccos* L., *Aster umbellatus* Mill. var. *pubens*

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Gray, *Solidago uliginosa* Nutt. Shrubs are scattered over the whole area, the principal species being *Potentilla fruticosa* L. and *Myrica Gale* L. The bog forest is of considerable extent and the trees are *Thuja*, *Larix*, and *Picea mariana*. Near the forest edge there is considerable sphagnum in hummocks much overgrown with grasses and other plants. The composite character of the vegetation in this locality is plain. It is certain that the change from swamp to bog conditions has been very gradual, and it is possible also that there has always existed here a slight element of bog vegetation.

THE SECONDARY SUCCESSION

The burn succession

I. Causes and extent of fires upon Isle Royale

During the period of mining activity upon Isle Royale fires were of frequent occurrence and many square kilometers were swept by them. Since the abandonment of the mines they have been much less frequent, so that most of the burned areas found today have already gone through a considerable period of forestward development. There is evidence that fires occurred long before the appearance of white men. A layer of burned wood deeply buried was found in the humus upon Smithwick Island, where otherwise absolutely no sign of burning was to be seen. Such fires must have been started either by Indians or by lightning. It is nearly certain that fire has played a part in the vegetational history of almost all if not the entire forested area of the island.

II. Effect of fire upon the climax forest

The effect of the destruction wrought by a forest fire is essentially to bring about a return to a more or less xerophytic condition, which is followed by a readvance leading again to the climax forest. The secondary development may be along the line of the original primary succession, but factors are usually present which bring about pronounced modifications in the process. Obviously the burn succession is exceedingly variable, and cannot be described in terms that will even approximately fit every case. The variable factor that is most important in creating differences in the succession is the severity of the fire. In respect to this two cases may be roughly distinguished.

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1. *Humus little harmed.*—This is the commonest type of burn upon Isle Royale and results in the development of a characteristic "burn forest" preceding the reestablishment of the climax. The composition of such a forest is mainly the outcome of the differing success with which the various species withstand the effects of the

FIG. 51.—Recently burned area on Smithwick Island: fireweeds dominant; a relict birch at the left; unburned forest in the background.

FIG. 52.—Young birch stump sprouts in a two-year-old burn near Siskowit Lake.

fire. The coniferous element of the climax forest, consisting of *Abies balsamea* and *Picea canadensis*, is entirely eliminated by a fire of any severity. *Betula alba* var. *papyrifera*, on account of its dry papery bark, is very inflammable, and the aerial portions are quickly destroyed. The underground parts, however, are not killed as are those of the conifers. They persist with great tenacity through most unfavorable conditions, provided the humus in which

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they are buried is unharmed, and are the most important contributors to the forest which immediately begins its development. *Pyrus americana* is similar to the birch in this respect, but is much less abundant. The shrubs of the climax forest seldom survive, though occasionally in a moist hollow a clump of *Taxus* will persist. The plants of the forest undergrowth, being close to the damp ground, frequently live through the fire. Some of them quickly succumb to the hard conditions which ensue, but certain species seem to thrive better than ever after the destruction of the forest cover. Prominent among the latter class are *Cornus canadensis*, *Linnaea borealis* var. *americana*, and *Maianthemum canadense*. These, which usually grow rather sparsely in the shade of the climax trees, come to cover large areas, flowering and fruiting luxuriantly. The first is one of the most characteristic species in the undergrowth of the burn forest.

Upon areas where the forest has been destroyed but the humus little harmed the progress of the burn succession is commonly as follows. During the first growing season after the fire those relicts which have survived renew their growth, and many new arrivals appear. Certain of the latter are much the most prominent features for a number of years. These are the familiar fireweeds, *Epilobium angustifolium* L. and *Anaphalis margaritacea* (L.) B. & H. (fig. 51).

Although the fireweeds give tone to the landscape for the first few years, the trees of the future forest begin their development equally early. The birches of the original stand, whose subterranean parts are still alive, sprout luxuriantly from the stump (figs. 52, 53). Often a ring of a dozen or more shoots appears where a single birch of the previous generation stood. Many of these die, but some develop into trees. Seedling birches and aspens (*Populus tremuloides*) add to the number, but upon Isle Royale the birch sprouts greatly predominate. The result is the development of a forest composed mainly of even-aged birches in clumps of 2–6 or more (fig. 54). A rich shrubby vegetation accompanies the trees. *Rubus idaeus* var. *aculeatissimus* is usually the first. *Diervilla Lonicera* Mill, *Corylus rostrata* Ait., and *Rubus parviflorus* Nutt. follow. When the birches have attained a size sufficient to produce

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moderate shade, the last named shrub (white-flowered raspberry) often forms a dense tall thicket growth beneath them. There is also a characteristic group of herbs that follow close upon the decline of the fireweeds. These are *Castilleja pallida* (L.) Spreng. var. *septentrionalis* (Lindl.) Gray, *Lilium philadelphicum* L., *Pteris aquilina* L., and others in the early stages; and *Aster macrophyllus* L., very abundant in the mature burn forest. A forest mainly of birches in clumps, with undergrowth as described above, is practically certain indication that fire has recently visited the area.

FIG. 53.—A group of birch stump sprouts in an area that was burned about 35 years ago: the original trunk is shown; near Park Place Hotel.

Frequently neighboring burns of different ages are indicated by patches of birch forest of differing height.

None of the areas of burn forest of historic age upon Isle Royale are old enough to show the late stages in the transition to the climax. The process is indicated, however, by the frequent occurrence of young spruce and balsam under the light shade of the birches. Occasional conifers germinate immediately after the fire, but the thorough occupation of the ground by the fireweeds and the rapid growth of the birch sprouts, as well as the dryness of the ground, prevent them from starting in abundance. The devel-

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opment of the burn forest is exceedingly rapid, thanks to the prolific sprouting of the birch, but the transition from burn forest to climax seems to be a slower process. Occasional areas of climax forest in which the birch element is mainly composed of groups of immense stump sprouts probably represent the penultimate stage in a burn succession following some prehistoric fire.

The effect of fire upon the composition of the flora is shown in table VI. The statistics were obtained from a study of areas of equal size in the unburned and burned portions of Smithwick

FIG. 54.—A young burned forest composed mainly of birches in clumps: the lower growth is *Juniperus communis* var. *depressa*, *Pteris aquilina*, and other species; near Park Place Hotel.

Island. The fire occurred about 15 years ago. The points to be noted are the destruction of the conifers and a part of the herbaceous flora, the increase of *Betula* and another portion of the herbaceous vegetation, and the appearance of *Populus*, *Rubus*, and the fireweeds.

2. *Humus destroyed; bare rock exposed.*—In such cases the reestablishment of the climax follows closely along the line of the rock shore succession, through lichen and crevice plant, and heath mat stages. Such differences as occur are due to the more thorough disintegration of the rock with greater abundance of soil materials

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resulting therefrom; the presence of more or less humus at the beginning (it rarely happens that fire destroys every vestige of organic matter, and even a very small quantity in a rock crevice is of great assistance in hastening the establishment of vegetation); frequent protection from the drying and mechanical effects of wind;

TABLE VI

Species	Climax forest	Burn
Abies balsamea	65	1
Betula alba var. papyrifera	6	117 (sprouts)
Picea canadensis	1	...
Pyrus americana	13	...
Populus tremuloides	..	16
Taxus canadensis	14	...
Viburnum pauciflorum	1	1
Rubus idaeus var. aculeatissimus	..	74
Aralia nudicaulis	21	...
Mitella nuda	21	...
Trientalis americana	13	...
Linnaea borealis var. americana	6	30
Clintonia borealis	2	...
Epilobium angustifolium	..	806
Anaphalis margaritacea	..	421
Maianthemum canadense	*	312
Calamagrostis canadensis	..	83

* Frequent in most parts of climax forest.

presence of a large body of invaders ready to advance from all directions. All these modifying influences tend to hasten the progress of the succession. Areas where fire has exposed the bare rock are found principally upon the tops of ridges, since the soil in such places is usually both shallow and dry, and whatever remains after the fire is washed away to lower levels.

III. Effect of fire upon the xerophytic and bog forests

When the jack pine–black spruce forest is burned, much of the humus is apt to be destroyed also, as the soil is commonly thin and dry. A few observations indicate that this type often succeeds itself. The pine grows faster and so for a number of years is the dominant tree. In one burned locality was found an open growth of pines 4–7 m. high, even-aged, averaging 28 years. Beneath

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them were scattered black spruces, few more than 1 m. high, also even-aged, and averaging more than a year older than the pines.

In extensive fires the patches of bog forest occupying the depressions often escape entirely because of abundant moisture. When they are burned over the coniferous element is destroyed, and the birches if present sprout from the stump. The underground portions of the two species of *Alnus* survive and renew growth, and the result is frequently a dense alder-birch thicket, which probably passes directly into the climax type. When the scattered trees growing upon an open bog are killed by fire the sphagnum, being usually saturated with water, seldom suffers severely. New bog trees begin growth and the succession goes on as before.

SUMMARY.—THE SUCCESSIONS

Primary successions

The xerarch successions

Every part of Isle Royale has at some point of its subaerial history been shore.

The present coast of the island is made up of rock shores and beaches, the former being much the more extensive. Each type possesses its characteristic series of successional stages, the ROCK SHORE SUCCESSION and the BEACH SUCCESSION, both resulting finally in the establishment of the climax forest.

With regard to area vegetated through its instrumentality, the rock shore succession is by far the most important of all the successions of Isle Royale.

The full series of the rock shore succession includes in its early stages three subsuccessions which later unite into a single series.

The *rock surface subsuccession* advances through crustose lichen and foliose lichen stages to a condition in which the large cladonias are the most important element. The process of invasion along this line alone is very slow.

The pioneers of the *crevice subsuccession* are certain herbs, notably *Potentilla tridentata*, whose principal rôle is the formation of humus. Trailing shrubs succeed them, the most important being *Juniperus horizontalis*, *J. communis* var. *depressa*, and *Arctostaphylos Uva-ursi*. These spread over the rocks from the

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crevices in all directions, and weaving among the cladonias and plants of the rock pools bring about the formation of a firm mat. The crevice vegetation is of extreme importance because of its rapidity of development and its preeminent part in the formation of the heath mat. Forest establishment is accomplished much sooner where crevices are abundant in the rock than where they are scarce.

The *rock pool subsuccession* goes through its development in depressions where water stands at least a part of the time. These become gradually filled after the manner of the bog succession, and the vegetation later becomes an element in the formation of the heath mat.

The *heath mat* results from the coalescence of the vegetation developed through the instrumentality of the three subsuccessions named above.

The *climax forest* often follows immediately after the formation of the heath mat, the trees obtaining their first foothold in the crevices. A relatively xerophytic forest stage characterized by *Pinus Banksiana* and *Picea mariana* sometimes intervenes, in which *Pinus* is the pioneer and *Picea* remains for some time after the climax trees have attained dominance.

Telescoping of stages is pronounced throughout the series, so that pioneer and climax forms, with those of all intermediate stages, are frequently found occupying a single limited area.

The effect of special conditions upon the rock shore succession is expressed in the two following laws:

1. The lower limit of possible forest extension is determined approximately by the upper limit of effective wave and ice work, the lake level remaining constant.

2. The extent to which the forestable territory has been occupied at the present day depends upon the rapidity of invasion, which is governed by the character of the rock, the angle of slope, and the degree of exposure to winds.

The operation of these laws results in the production of three phases of rock shore vegetation, characterized respectively by (*A*) climax forest to the water's edge, (*B*) a zone of incomplete invasion, (*C*) abrupt transition from bare rock shore to climax forest.

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During the early subaerial history of Isle Royale the rock shore succession may have differed from that of the present day. A study of Gull Islands indicates that birds may have been important agents in determining the composition of the primitive rock shore flora of the island.

The beaches on account of their sheltered location usually bear the climax forest down to its limit of possible extension. Low shrubs of various kinds are the most important pioneers in the beach succession, and larger ones, especially *Alnus crispa*, intervene before the establishment of the climax type.

The hydrarch successions

The bog succession

Physiographic development.—The depressions which now contain lakes or bogs owe their origin to glacial modification of the preglacial topography; sometimes to the cutting off of bays or channels by wave-built bars.

The physiographic history of the habitat in which the bog succession runs its course comprises two stages: the channel-bay stage and the lake stage. The lakes and harbors are tending toward extinction through the agencies of down-cutting of outlets, sedimentation, and vegetation, of which the last is the only one of importance at the present time. The lake stage ends when vegetation, aided by the other agencies, has entirely eliminated the open water.

Vegetational development.—During the channel-bay stage aquatics first appear and gradually increase with increasing shelter; the beginnings of the sedge mat are occasionally present.

During the physiographic lake stage all the vegetational stages of the succession appear in order: aquatics (usually already present), sedge mat, sphagnum-shrub, bog forest. All may have their beginnings at practically the same time. The sedge mat is usually the most prominent feature at this period. The sedges gain their first foothold in shallow water close to shore and build a floating mat out over the water. They are by far the most important agents in peat formation.

During the covered bog stage the plant societies are successively eliminated by the centripetal encroachment of the various zones.

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Two lines of succession are distinguished after the sedge mat stage. One is characterized by *Chamaedaphne*, *Andromeda*, and *Alnus incana* in the shrub stage, practical absence of sphagnum, and by *Larix* and sometimes *Thuja* in the bog forest; the other by *Chamaedaphne* and *Andromeda* followed by *Ledum* in the shrub stage, abundance of sphagnum accompanying the shrubs, and by *Larix* and *Picea mariana* in the bog forest. Sphagnum is the critical plant in the differentiation of the two series, since *Ledum* and *Picea mariana* appear later, and only in cases where sphagnum is abundant. The differences may be related to differences in drainage, since those bogs containing little sphagnum are usually well drained, while in those with abundance of sphagnum, as far as observation has gone, drainage was very poor or lacking entirely. A contributing factor is found in differences in the composition of the sedge mat preceding the shrubs and sphagnum. In the sphagnum bogs *Carex limosa* is the principal mat-forming species. Being low and soft, it offers no resistance to the spread of the moss. In the bogs with little sphagnum *Carex filiformis* is the important mat-former. On account of its height and stiffness and dense growth it produces unfavorable conditions for the spread of sphagnum. The reason for the differing distribution of the two carices is unknown; it may be merely accidental.

The sphagnum is a superficial layer supported upon the sedge mat, and contributes little toward peat formation. It begins growth some distance within the bog margin and spreads both ways, slowly toward the margin, faster centerward. The area between the sphagnum and the upland commonly forms a marginal trench. In some places the moss by recent invasion has obliterated the marginal trench, and occasionally it transgresses the bog margin, spreading up the forest floor for several meters.

The sphagnum spreads marginally, surrounding and smothering such plants as cannot keep pace with its growth. Certain species by upward elongation are able to survive for some time, especially *Andromeda* and *Chamaedaphne*, the latter persisting longest.

Ledum almost invariably follows the sphagnum, and its root system is usually strictly confined to the masses of it. It forms a

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very dense growth, and through its shading power and the great amount of waste that falls from it finally eliminates the lower shrubs and stops the upward growth of the moss.

The bog trees, *Larix*, *Thuja*, *Picea mariana*, usually follow the sphagnum when it is present. When it is lacking they start upon the sedge mat with the shrubs. The climax trees enter very soon after or often actually with the bog trees, so that pure bog forest is practically absent. The bog trees die out because they are intolerant of shading, and the climax forest results.

Telescoping of stages is prominent throughout the late history of the succession.

The reason for the early establishment of the climax forest is found in the likeness between the bog soils and those of the forested uplands, the latter being almost as peaty as those of the bogs. It follows that whatever trees can grow upon one soil may also exist upon the other.

The delta swamp succession

Delta deposits are found in most of the sheltered bays where streams enter from the upland.

The succession of vegetation upon these deposits passes through the following stages: (1) aquatics; (2) sedges; (3) grasses (*Calamagrostis canadensis* most important), which form broad meadow-like growths and produce a limited amount of peat; (4) shrubs, among which *Myrica Gale* and *Alnus incana* are most important; (5) swamp forest, made up of *Thuja occidentalis*, *Larix laricina*, and *Fraxinus nigra*, the first being dominant; (6) climax forest of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*.

There is a general likeness to the bog succession; among other points, in the early establishment of the climax forest after the coming in of the swamp trees.

The important points of difference from the bog succession are: the firmly grounded sedge mat; interpolation of the grass stage; absence of sphagnum, bog shrubs, and *Picea mariana;* dominance of *Thuja* in the swamp forest.

Intermediate conditions between the two successions occur, and actual transition from delta swamp to bog succession occasionally takes place.

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Secondary succession

The burn succession

The effect of fire upon the climax forest is to bring about a return to a more or less xerophytic condition, which is followed by a readvance leading to the climax. Two general cases may be distinguished.

1. *Humus little harmed.*—The coniferous element is destroyed, but the birches survive in their underground portions and sprout abundantly from the stump, usually producing a nearly pure

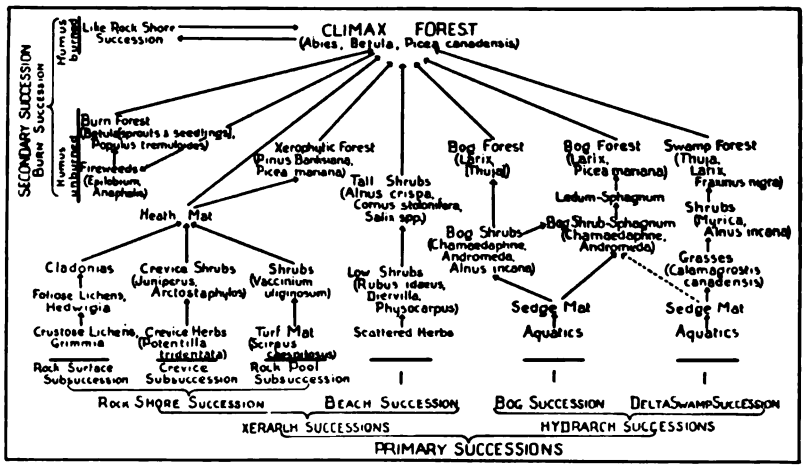

FIG. 55.—Diagram to illustrate the courses of the various successions upon Isle Royale.

forest of birches growing in clumps. Seedling birches and aspens are usually present also. Conifers gradually return, finally bringing about the reestablishment of the climax.

2. *Humus destroyed; bare rock exposed.*—The reestablishment of the climax follows closely along the line of the rock shore succession, but progress is usually more rapid because of the presence of soil materials and numerous invaders, and frequently protection from wind.

The courses of the various successions and their relations to each other are shown graphically in the diagram (fig. 55).

PALO ALTO, CALIFORNIA

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STUDIES ON THE PHLOEM OF THE DICOTYLEDONS

II. THE EVOLUTION OF THE SIEVE-TUBE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 169

ANSEL F. HEMENWAY

(WITH PLATE XI AND THREE FIGURES)

In 1909–10 the writer studied the phloem of some 30 species of lower dicotyledonous trees and found that the sieve-tubes in these species had the same general structure as those of the gymnosperms or vascular cryptogams.[1] Some 60 species of higher woody dicotyledons were investigated the next year, and this last year about 90 species of herbaceous dicotyledons and 12 monocotyledons have been studied.

As the literature on the subject of phloem has been rather well reviewed and catalogued recently, an exhaustive review of it will not be given here. In 1908 HILL[2] gave a good review of the literature from the histological standpoint. MANHAM[3] similarly discusses the literature from the physiological side. CHAUVEAUD[4] in an extensive paper gives a brief review of the literature of phloem.

The material for this investigation was collected in late summer or early fall, the object being to get the sieve-tubes in mature condition, so that they would best show callus formation. For the sake of comparison, several species were studied in seedling condition and in the adult growing condition.

Before proceeding to the discussion of the evolution of the sieve-tube, a few general observations on phloem anatomy may well be mentioned. The distribution of the hard bast in the woody

[1] HEMENWAY, ANSEL F., Studies on the phloem of the dicotyledons. I. Phloem of the Juglandaceae. BOT. GAZ. 51:131–135. *pl. 13.* 1911.

[2] HILL, A. W., The histology of the sieve-tube of angiosperms. Ann. Botany 22:245–290. *pls. 17, 18. figs. 13.* 1908.

[3] MANHAM, S., The conduction of carbohydrates. Science Prog. Oct. 1910 and Jan. 1911.

[4] CHAUVEAUD, G. L., L'appareil conducteur des plantes vasculaires et les phases principales de son évolution. Ann. Sci. Nat. Bot. IX. 13:113–438. *figs. 218.* 1911.

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dicotyledons is very characteristic for each species and usually for each genus. In many cases it is arranged in bands concentric with the cambium, as in *Acer*, *Populus*, and *Crataegus;* in some cases in groups opposite the large or aggregate rays, as in *Alnus*, *Carpinus*, and *Drimys;* in other cases in irregular patches, as in *Ostrya* and *Celtis;* and finally, in various combinations of these arrangements, as in *Quercus*.

Plate figs. 1–3 show some of these peculiarities of phloem structure. Fig. 1 is a transverse section of *Acer macrophyllum;* the lighter horizontal bands are the hard bast cells; between these are the sieve-tubes and parenchyma cells; while the dark vertical lines are the phloem rays; in the lower portion of the figure the cambium and some xylem are seen. Fig. 2 is a similar view of *Alnus incana;* here we note that the hard bast occurs chiefly opposite the aggregate ray. Fig. 3 is a similar view of *Quercus Garryana;* a large group of hard bast is seen above the large ray in the lower left portion of the figure, while several smaller groups appear here and there in other parts of the phloem.

Fig. 4 is a transverse section of the stem of *Ranunculus fascicularis;* the central, lighter portion of the three bundles shown here is phloem. Fig. 5 is a similar view of *Chenopodium album*, and fig. 6, of *Amaranthus paniculatus*. The darker areas just above the groups of large vessels are phloem. This peculiar, scattered arrangement of bundles in a woody cylinder would suggest a possible point of origin for the monocotyledons.

Companion cells are rare if not wanting in many of the lower dicotyledons. It is probable that parenchyma cells play the part of companion cells here.

The end walls of the ray cells in the phloem of some woody dicotyledons show sieve-platelike pitting, but they did not show any callus formation. This formation is easily observed in tangential sections of *Phellodendron*, *Rhus*, *Ilex*, *Acer*, *Gymnocladus*, *Acanthopanax*, and many other species. There are often thick-walled, unlignified, phloem-parenchyma cells in both woody and herbaceous dicotyledons that show lateral sieve-platelike pittings, but no terminal sieve-plates or callus were seen.

In the herbaceous dicotyledons studied, often the most striking

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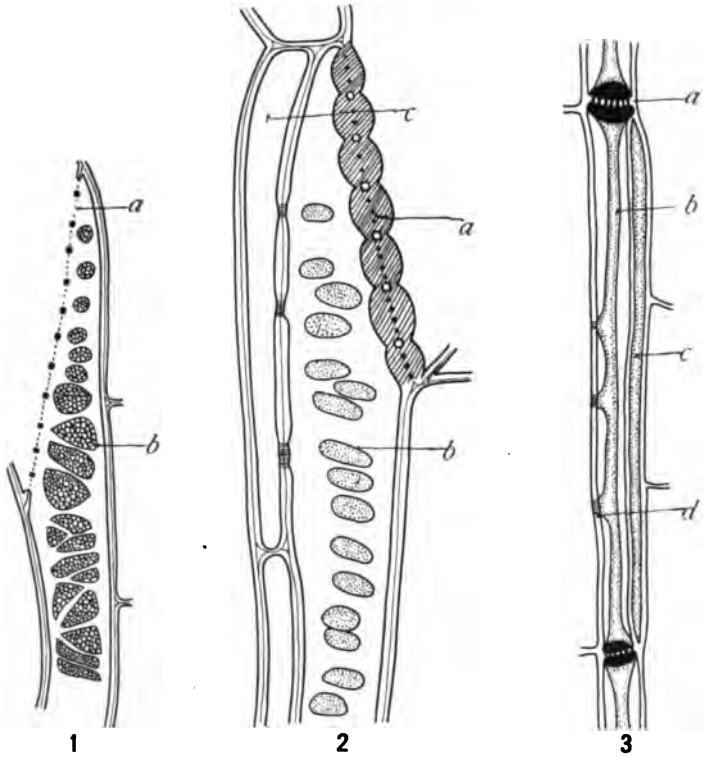
feature was the relatively small amount of phloem present. In *Paeonia* and *Thalictrum*, for example, there may be only 6–12 sieve-tubes in a bundle having perhaps 30–50 times that number of xylem elements; but often in woody plants only a few rows of sieve-tubes, as seen in radial section, are really functional.



FIGS. 1–3.—Fig. 1, one-third of a sieve-tube of *Juglans nigra:* *a*, end sieve-plate in cross-section; *b*, lateral sieve-plate in face view; fig. 2, one-half of a sieve-tube of *Vitis labrusca:* *a*, end sieve-plate in cross-section: *b*, lateral sieve-plate in face view; *c*, companion cell; fig. 3, full length view of a sieve-tube of *Lactuca scariola:* *a*, end sieve-plate in cross-section, with callus; *b*, slime contents; *c*, companion cell; *d*, lattice or "sieve-field."

No lignification of the phloem was observed in *Helianthus*. Perhaps the material used was collected too early or grew under different conditions from that described by BOODLE.[5]

[5] BOODLE, L. A., Lignification of phloem. Ann. Botany **16**: 180. 1906; also *ibid.* **20**: 319–321. 1910.

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Species of over 140 genera, belonging to more than 60 families, have been studied. The sieve-tubes found in these different species, for the sake of convenience, may be grouped under three types, though perhaps most of them will come naturally between the first and second or second and third types.

The first type is like that found in *Pinus*. Here the lateral sieve-plates are the same as the terminal ones, and the end walls are very oblique, extending from one-fourth to one-half the length of the sieve-tube. Text fig. 1 shows one-third of a sieve-tube of *Juglans nigra* as seen in tangential view. The lateral sieve-plates are seen in face view on the tangential wall, while the terminal sieve-plates are seen in transverse section. The lateral sieve-plates on the tangential walls of the sieve-tubes in *Juglans* are usually more irregular and thinner than those on the terminal or radial walls.

The second type is like the first except that the lateral sieve-plates are less well developed, and the end walls are less oblique, and have 2–10 sieve-plates each. This type may be illustrated by *Vitis* (text fig. 2). The figure shows one-half of a sieve-tube in tangential section. The end wall here has 7 sieve-plates covered with callus. Poorly developed sieve-plates are shown in face view on the tangential wall. On the left is a companion cell related to the sieve-tube by fine pits.

The third type has end walls that are nearly at right angles to the side walls, and has only one sieve-plate to each end wall. The sieve-tubes of *Lactuca scariola* illustrate this type (text fig. 3). This sieve-tube, though shown in full length view, was drawn to the same scale as the other text figures. The three lattices on the left relate it to another sieve-tube.

The species studied may be grouped under these types as follows:

FIRST TYPE[6]

Alnus incana, A. rugosa, A. oregana, Betula alba, B. lenta, B. lutea, Banksia Menziesii, Carya alba, C. ovata, Castanea dentata, Castanopsis chrysophylla, Casuarina Fraseriana, C. equisetifolia, Corylus americana,

[6] The nomenclature of GRAY'S *Manual* (Ed. 7) is followed as far as applicable; the names of plants indigenous to Oregon are those used in HOWELL'S *Flora of Northwest America*.

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C. rostrata, Carpinus caroliniana, Drimys colorata, Fagus grandifolia, Juglans cinerea, J. nigra, Myrica asplenifolia, M. cerifera, Nothofagus Menziesii, Ostrya virginiana, Populus balsamifera, P. grandidentata, P. tremuloides, P. trichocarpa, Quercus alba, Q. Garryana, Q. Kelloggii, Q. nigra, Salix fragilis, S. nigra.

BETWEEN FIRST AND SECOND TYPES

Berberis aquifolium, Celtis occidentalis, Aesculus glabra, A. Hippocastanum, Acer Negundo, A. macrophyllum, A. rubrum, A. saccharum, Crataegus coccinea, C. Douglasii, Calycanthus floridus, Fraxinus americana, F. oregana, Hamamelis virginiana, Holodiscus ariaefolia, Hydrangea vestita, Liriodendron Tulipifera, Magnolia acuminata, M. Fraseri, Maclura pomifera, Morus rubra, Philadelphus Lewisii, P. grandiflora, Platanus occidentalis, Prunus serotina, Pyrus baccata, P. coronaria, Rosa gallica, Ribes sanguineum, Sassafras variifolium, Ulmus campestris, U. americana.

SECOND TYPE

Ailanthus glandulosa, Arbutus Menzesii, Catalpa bignonioides, Ceanothus sanguineus, Cephalanthus occidentalis, Cercis canadensis, Cladrastis lutea, Cornus Nuttallii, C. pubescens, Clethra alnifolia, Diospyros virginiana, Euonymus atropurpureus, Gymnocladus dioica, Gleditsia tricanthos, Ilex opaca, Kalmia latifolia, Lyonia ligustrina, Phellodendron amurense, P. japonicum, Robinia Pseudo-Acacia, Rhus glabra, R. Toxicodendron, Ricinus communis, Rhamnus cathartica, R. Purshiana, Sambucus glauca, Syringa vulgaris, Tilia americana, T. europaea, Vaccinium corymbosum, Vitis labrusca.

BETWEEN SECOND AND THIRD TYPES

Abutilon Theophrasti, Acanthopanax sessiliflorum, Actaea alba, Agrimonia gryposepala, Amaranthus paniculatus, Aquilegia formosa, A. vulgaris, Aralia spinosa, Asarum canadense, Asclepias syriaca, Chenopodium album, Clematis ligusticifolia, Brassica alba, Datura stramonium, Daucus Carota, Dipsacus sylvestris, Euphorbia Preslii, E. corollata, Filipendula rubra, Geranium sanguineum, Geum triflorum, Hibiscus Moscheutos, Hypericum perforatum, Humulus Lupulus, Impatiens noli-tangere, I. pallida, Knautia arvensis, Paeonia montana, Potentilia rivalis, Polanisia graveolens, Polygonum Douglasii, Raphanus sativus, Rumex occidentalis, Saponaria officinalis, Solanum nigrum, Thalictrum dasycarpum, Tropaeolum majus, Urtica gracilis, Verbena officinalis.

THIRD TYPE

Ambrosia artemisiifolia, Arctium minus, Aster novae-angliae, Bryophyllum calycinum, Cichorium Intybus, Cicuta maculata, Cucurbita maxima, Cyclamen latifolium, Eupatorium purpureum, Echinocystis lobata, Eryngium yuccifolium, Helianthus annuus, Heracleum lanatum, Hieracium venosum, Lactuca scariola, Liatris squarrosa, Linaria vulgaris, Lobelia cardinalis,

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Lupinus polyphyllus, Melilotus alba, Monarda punctata, Oenothera biennis, Opuntia Rafinesquii, Phaseolus vulgaris, Phytolacca decandra, Physalis heterophylla, Primula sinensis, Sium cicutaefolium, Scrophularia marilandica, Silphium laciniatum, Sonchus oleraceus, S. arvensis, Stachys palustris, Tephrosia virginiana, Trifolium pratense, Verbascum Thapsus, Veronica scutellata, Xanthium spinosum.

The following monocotyledons were similarily studied, and all were found to have sieve-tubes of the third type.

Alisma Plantago, Arisaema triphyllum, Dracaena scandia, Iris versicolor, Monstera deliciosa, Polygonatum commutatum, Potamogeton heterophyllus, Sagittaria latifolia, Scirpus validus, Smilax rotundifolia, Typha latifolia, Zea Mays.

There are of course no sharp lines of division in grouping these species according to type; even in the same section there may be some variation. But in general there is no wide variation even with different genera of the same family, except where there are both woody and herbaceous genera; then the herbaceous ones showed the higher type, as for example in Rosaceae and Leguminosae. The sieve-tubes of the Leguminosae on the whole are of a higher type than those of the Rosaceae. The woody Rosaceae often have sieve-tubes about like the first type, with regular large lateral sieve-plates. While the woody Leguminosae may have occasionally well developed lateral sieve-plates, they are usually as small as in *Sambucus* or *Tilia*. The xylem of the Leguminosae has been likewise found to be a higher type, so perhaps these families do not belong so near each other as they are usually placed.

It will be noted that the woody dicotyledons studied are placed in the first and second types, while the herbaceous ones are in the intermediate type between the second and third, or in the third type. Three or four sieve-plates were the most seen on the end wall of any strictly herbaceous plant, as for example *Euphorbia* and *Thalictrum*. Even in these genera end walls with only one sieve-plate were often observed. In the Compositae studied, only one sieve-plate to each end wall of the sieve-tube could be found. When stained with RUSSOW'S callus reagent, the pores of the "sieve-fields" or lattices showed up as orange dots, but they never were large nor fused into callus pads.

Occasional lateral callus pads were observed in most of the

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other herbaceous plants studied. In *Cucurbita maxima*, for example, as many as 9 lateral callus pads have been seen in a continuous row in a single sieve-tube.

The evolution of the sieve-tube parallels that of the tracheid or vessel. For example, in *Ephedra* the vessels have oblique end walls with several round or oval pits. This is supposed to be the primitive type of vessel. In *Liriodendron* the end wall of the vessel is still rather oblique, but the pits are of the scalariform type and close together. In the highest type, the pitted vessel, the little margin that is left of the end wall is usually at right angles to the side walls, as in *Fraxinus*.

Conclusion

In studying the phloem of the dicotyledons, it has been found that there is a gradual transition from the gymnospermous type of sieve-tube to the so-called dicotyledonous type as seen in the Compositae. At the first stage in advance the lateral plates are smaller and have smaller meshes than the terminal plates; then as the terminal wall becomes more and more at right angles to the lateral walls, the number of terminal plates decreases until there is only one terminal plate with relatively large meshes, and the lateral plates become "sieve-fields" or lattices.

Paleobotany, ontogeny, and studies of xylem have induced many botanists to believe that herbaceous plants are more advanced in their evolutionary development than woody plants. This study of the sieve-tube adds another argument in favor of this view.

The first two years of this work were done in the Phanerogamic Laboratory of Harvard University under the direction of Professor E. C. Jeffrey, and the last year of work has been under the direction of Professors J. M. Coulter and W. J. G. Land at the University of Chicago. The writer wishes to express his thanks to these instructors for their helpful advice.

Transylvania University
Lexington, Ky.

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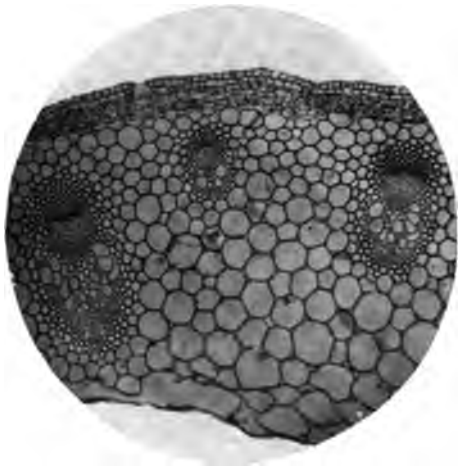

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EXPLANATION OF PLATE XI

FIG. 1.—Transverse section of phloem of *Acer macrophyllum*, showing horizontal bands of hard bast and general view of sieve-tubes and parenchyma cells.

FIG. 2.—A similar view of *Alnus incana*, showing that the hard bast occurs chiefly opposite the aggregate rays.

FIG. 3.—A similar view of *Quercus Garryana*, showing distribution of hard and soft bast.

FIG. 4.—Transverse section of stem of *Ranunculus fascicularis*, showing scattered bundles and relatively small amount of phloem.

FIGS. 5 and 6.—*Chenopodium album* (fig. 5) and *Amaranthus paniculatus* (fig. 6), showing peculiar scattered bundles that might suggest relationship to the monocotyledons.

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PARAFFIN BLOCKS FOR GROWING SEEDLINGS IN LIQUID CULTURE SOLUTIONS[1]

CONRAD HOFFMANN

(WITH THREE FIGURES)

In growing seedlings of any kind in nutrient solutions a suitable means of supporting the individual plants is essential. The method commonly employed consists in the use of ordinary corks perforated so as to hold a varying number of seedlings. Invariably the corks are of such a size as to fit snugly in the neck of the vessel containing the nutrient culture solution. This apparatus, while satisfactory to a certain extent, offers several objections. The corks usually discolor the nutrient solution, the extent of discoloration depending upon the grade of cork employed, as well as upon the composition of the nutrient solution. This discoloration is due to soluble compounds, presumably organic in nature, which can be inferred to have some influence—beneficial or detrimental—upon the growing seedlings. The corks soon warp and crack and become unfit for further use. Further than this, they furnish a substratum for molds, which frequently give trouble by infecting the seedlings to be grown.

These were some of the objections and difficulties encountered in the course of certain experimental work with growing seedlings. It was necessary in this work to grow a large number of seedlings in different culture solutions, which necessitated the employment of a large number of supports. The support which was finally adopted after considerable experimentation proved so satisfactory as to warrant its description and publication at this time.

In place of the ordinary cork a paraffin block molded in the desired shape and size and perforated to suit the needs of the experiment has been used. It has been found advisable to employ a paraffin of comparatively high melting point, so as to prevent any melting or softening of the blocks under the direct rays of the sun to which they will be exposed in the course of their use.

[1] Published with permission of Director of Wisconsin Experiment Station.

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To obtain blocks of the desired thickness and size, the following procedure has proved most effective. The paraffin is placed with sufficient distilled water in a suitable vessel and boiled vigorously. The paraffin can then be removed from the surface of the water

FIG. 1.—Showing use of paraffin block and hydrometer cylinder for growing seedlings in nutrient solutions.

and poured into a large cylindrical mold. This mold is best made out of some heavy paper and can be made of any desired diameter. After solidification of the paraffin within this mold, the various-sized cylinders can be cut off in much the same manner that bread

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is cut. These cylindrical blocks can be made of any thickness, and by varying the size of the mold can be made of any diameter. To render the cutting of the paraffin more satisfactory, the mold can be placed at a temperature of 30–35° C., which will be sufficient to keep the paraffin in a pliable condition. Another method for securing these blocks which has given good satisfaction is to pour the hot water and paraffin into shallow pans, forming a layer of paraffin above the water of any desired depth, and then allowing it

FIG. 2.—Seedlings in paraffin blocks suspended in water to show root development

to solidify. From the circular layer thus secured, the desired blocks can be cut with various-sized cake cutters.

The blocks of paraffin thus secured are then perforated in one of two ways. In the one the ordinary cork-borer is employed, using two of different diameters, making a perforation with the smaller through the entire block, and then with the larger borer through the upper portion of the block. In this way a perforation is secured with a small shelf upon which the germinating seedling can be placed. Equally satisfactory has proved the method of

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using a piece of ordinary glass tubing which has been drawn out in a conical form. By pushing this through the paraffin a perforation is secured which is larger at the top and smaller at the bottom of the block, and which will prevent the seed from falling through into the liquid in which the paraffin blocks are to be suspended. In this manner one can make a support of any size and with as many perforations as desired. These blocks when placed in the liquid culture medium serve automatically to keep the roots immersed

FIG. 3.—Same seedlings as in fig. 2, but removed from water; far less differentiation in root development is evident.

in the liquid, since they are free to rise and fall with variations in the level of the nutrient solution. This is impossible with a cork which fits snugly in the neck of the vessel, unless one continually restores the water lost by transpiration and evaporation.

The size of the block, as well as the perforations, will depend entirely upon the seedlings to be grown, making them large for peas and corn, and small for wheat and clover. The blocks thus prepared can be floated upon the culture medium in which the seedlings are to be grown, and, as already stated, will rise and fall

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with changes in the elevation of the nutrient solution. Sufficient bulk must be given to the blocks to provide for the increased weight resulting from the growth of the plant.

The most suitable receptacle for floating these block cultures has been found in the form of an ordinary hydrometer cylinder which has the enlargement at the upper portion of the cylinder. This is well shown in the accompanying illustration (fig. 1).

For photographic purposes of seedlings thus grown these floats with their burden are placed in large, flat, glass vessels similar to the rectangular museum jars which are now being employed. In this way the root systems are well distributed and give a photograph revealing any differences which may exist in the root development. A comparison of the two photographs submitted (figs. 2 and 3), the one taken as above described, the other after removal from the water demonstrates this feature very strikingly, and proves the advantages of photographing as described. This method of photographing is considered worthy of employment where work of a similar nature is performed and presented.

AGRICULTURAL BACTERIOLOGICAL LABORATORIES
UNIVERSITY OF WISCONSIN, MADISON, WIS.

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BRIEFER ARTICLES

A SIMPLE REVOLVING TABLE FOR STANDARDIZING POROUS CUP ATMOMETERS

(WITH ONE FIGURE)

In connection with field work carried on during the past season the writer has had occasion to standardize nearly 70 porous cup atmometers of the type described by LIVINGSTON.[1] The necessity of exposing the various cups in a series to uniform atmospheric conditions during the standardizing process is readily comprehended, but the difficulty in securing such conditions can be fully appreciated only by those who have tried it. LIVINGSTON has recently described a rotating table for standardizing these instruments,[2] and so far as fulfilling the requirements is concerned this can scarcely be improved upon. The only objection to it is the amount of time and expense involved in its construction, an objection which may have considerable weight if what is needed is a makeshift contrivance for temporary or perhaps occasional use rather than a durable piece of permanent equipment. The writer has devised for his purpose a very simple type of revolving table which can be constructed from readily obtainable materials with very little labor and expense and which has proven very serviceable.

This apparatus is shown in the accompanying photograph (fig. 1). It consists, in brief, of the front wheel of a bicycle suspended horizontally within a wooden framework; on the upper side of the wheel is laid a piece of thick cardboard, or pulpboard, to support the bottles; from the lower side of the wheel wooden vanes are hung perpendicularly; the wheel is then caused to rotate by means of an air current from an electric fan. For constructing the framework three-quarter inch pine board is sufficiently heavy, and rigidity is insured by the use of braces at the angles; the dimensions are largely a matter of convenience and will naturally depend somewhat on the diameter of the wheel used, height of atmometers, size of vanes, etc.; the framework shown in the figure measures 36×30×24 inches (inside height, inside width, and depth, respectively). For supporting the wheel two upright pieces are

[1] Carnegie Institution of Washington, Publication No. 50. 1906.

[2] Plant World 15: 157–162. 1912.

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used; one of these projects vertically upward from near the center of the base of the framework (see fig. 1) to a level somewhat less than halfway to the top; the other projects downward from the top of the framework, in line with the first, to a level somewhat less than halfway to the bottom; the distance between the two contiguous ends of these uprights should be slightly greater than the length of the wheel hub; both uprights should be firmly braced. The wheel is held in position between the two uprights by means of two iron "corner-braces" (which can be secured at any hardware store), in each of which one of the four screw holes has been bored large enough to fit the axle of the wheel. In adjusting the

FIG. 1

wheel to position a corner-brace is first screwed vertically to the upper end of the lower upright; the wheel is set in this and then firmly fixed in place by means of the second corner-brace which is screwed to the lower end of the upper upright; any slight divergence of the wheel from the horizontal plane can be corrected later by tilting the entire framework. For vanes 8 pieces of light wood about 8×10 inches are used; these are attached to the spokes by means of screw-hooks, being hung at a slight angle to the radii of the wheel; they are tied to the rim at their upper edges and are further held in position by means of wooden strips tacked to their lower edges. This table will accommodate 20 or more atmometers. As a precaution against the possibly disastrous

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effect of centrifugal force it is well to fasten a cord around the bottles after the manner shown in the figure. The velocity at which the table rotates can be controlled by regulating the position and angle of the fan with respect to the vanes. If the bearings of the wheel are properly adjusted and the table with its load carefully balanced, a speed of less than four revolutions per minute can be maintained. The direct air current from the fan should not strike the cups.

Such a revolving table as the one here described was run in the writer's laboratory almost continuously for nearly three weeks at a speed ranging from 4 to 20 revolutions per minute and gave no trouble whatever. In order to determine the accuracy of the data obtained, a test series of 20 cups was operated under various conditions for more than a week, readings being taken daily. It was found that with the table revolving at a rate of 8 revolutions or less per minute the coefficients derived from the readings of consecutive days varied very little; for several days none of the cups showed a variation amounting to as much as one per cent, while the difference in evaporation between two standard cups amounted to less than 0.2 per cent. With increased speed, however, the coefficients are apt to fluctuate, due to various causes.—G. E. NICHOLS, *Yale University*.

POISONING BY GINKGO

Several botanists after dissecting the fruits of *Ginkgo* have developed what appeared to be ivy poisoning. As the juice of the *Ginkgo* produced an immediate irritation of the skin, it was suspected that the rash which developed the following day was due to this. Later tests proved this to be the case. The poison is in the outer fleshy layer. It does not affect all people, since the gardeners at Smith College and at Mount Holyoke College have never been poisoned by handling the *Ginkgo* fruits, but a gardener in Elyria, Ohio, who cares for a fruiting tree in the yard of Mr. WILLIAM G. SHARP, writes that he is poisoned every fall by handling the fruits. The irritation produced is greater than that of poison ivy, and the infection spreads more persistently and is communicated from one person to another. Pustules rarely form, however, as in ivy poisoning, but there is a heavy red rash, attended by the formation of welts in severe cases.—ANNA M. STARR, *Mount Holyoke College, South Hadley, Mass.*

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CURRENT LITERATURE

BOOK REVIEWS

Parasitic seed plants

In order to place at the command of students and teachers the best known methods of growing parasitic seed plants and to encourage the introduction of these hitherto neglected organisms into botanic gardens, HEINRICHER[1] has compiled from his wide experience a manual of explicit directions for the culture of all the better known species. Most of the European and many of the foreign representatives of the Scrophulariaceae, Orobanchaceae, Convolvulaceae, Lauraceae, Santalaceae, Loranthaceae, and Rafflesiaceae are included in his rather extensive list, and in nearly every instance his suggestions are based upon personal experience extending over several years. His previous investigations of the peculiarities in the germination of the seeds of parasites (reviewed in this journal[2]) have been extended, and much valuable data collected on the time required for bringing the parasites to maturity, as well as to the particular host upon which each develops best. While many of these plants may be grown readily in the open ground, pot culture is recommended for others on account of the greater ease with which they may be protected from insects and other enemies. It is found that many of the green hemiparasites are not very exacting in their choice of a host, but in promoting vigorous and rapid development care is often necessary in selecting a host that will not by too vigorous growth exclude the sunlight from the foliage of the parasite. This would indicate that the dependence is here incomplete and that carbohydrates are synthesized by the leaves of the parasite. HEINRICHER, however, does not rely upon this evidence alone to demonstrate that many of the green parasitic seed plants, particularly those of the Rhinanthaceae, obtain only water and nutritive salts from their hosts, but produces what seems to be a most complete line of evidence in support of his contention[3] that photosynthesis continues long after the evolution of the parasitic habit has begun. He presents evidence that the leaves of these plants are highly differentiated morphologically, possess abundant stomata,

[1] HEINRICHER, E., Die Aufzucht und Kulture der parasitischen Samenpflanzen. 8vo. pp. 53. Jena: Gustav Fischer. 1910.

[2] BOT. GAZ. 49:391. 1910.

[3] HEINRICHER, E., Die grünen Halbschmarotzer, VI. Zur Frage nach der assimilatorischen Leistungsfähigkeit der grünen parasitischen Rhineanthaceen. Jahrb. Wiss. Bot. 47:539–587. 1910.

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show a periodicity in their starch content which coincides with the recurrence of daylight and darkness, that locally darkened areas of the leaf blade soon show a deficiency in starch content, and that when the stomata are closed with cocoa butter starch formation does not occur. Further it appears that shoots free from starch soon showed the presence of that substance if placed in sunlight in an atmosphere containing CO_2, but controls, also in sunlight but in an atmosphere without CO_2, showed no starch. Support is also given to the contention that many of these plants receive no carbohydrates from their hosts by the fact that they will thrive as root parasites upon annuals which have no starch or sugar stored in their subterranean organs.—GEO. D. FULLER.

Phosphorescence in plants

MOLISCH[4] has issued a second and enlarged edition of his work on phosphorescing plants. The book is very simply and interestingly written, and brings up to date his own extensive work in this field as well as the work of all other investigators. The first chapter answers negatively the question "are there phosphorescing algae?", and shows that such appearances are due to light reflection or to animals living on the algae. The second chapter gives the evidence for the existence of phosphorescence in marine Peridineae and for its absence in fresh water forms. The third chapter deals at length with the phenomenon in fungi, both Hyphomycetes and bacteria, and the fourth shows the relation of salts and temperature to the light production in bacteria. The fifth treats of the nutrition, phosphorescing, and growth of the light-producing fungi, and the sixth with the manner in which light is produced. Phosphorescence is an oxidation process demanding a minimal though very small partial pressure of oxygen. There is no convincing evidence for any direct relation between respiration and phosphorescence, much less for the latter being produced by the former. The living cell produces a substance, photogen, which phosphoresces in the presence of water and free oxygen. In the higher fungi and bacteria, in contrast to many animals, the phosphorescing has never been obtained extracellularly. In chapter seven the author gives the spectra and other characters of the light produced by various fungi.

The bacterial light is of sufficient intensity and of proper quality to render photographic work possible by it as the sole source of light. It will cause heliotropic response in various seedlings and fungi, and lead to chlorophyll production, detectable by the spectroscope though not sufficient for visible greening. The light is not capable of penetrating opaque objects, as some workers have probably wrongly claimed for light produced by various animals.

In contrast to the situation with many animals, MOLISCH cannot discover any biological significance of light production in plants. The last chapter

[4] MOLISCH, HANS, Leuchtende Pflanzen, eine physiologische Studie. viii+193. *pls. 2. figs. 18.* Jena: Gustav Fischer. 1912.

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deals with the alleged phosphorescence in flowering plants, and concludes that the cases cited are either counterfeit or due to electrical phenomena (St. Elmo's fire).—WILLIAM CROCKER.

MINOR NOTICES

The nuclei of Protista.—The name "Protista," applied by HAECKER to the lowest animals and plants, has failed to receive general acceptance, even among zoologists, and the forms are found under both the protozoa and unicellular plants. In any consideration of the phylogeny of the nucleus these forms must be of great interest, because the nuclei of the metazoa and of the higher algae and fungi are too highly differentiated to throw much light upon such a subject as the origin of the nucleus. A paper by HARTMAN[5] deals almost entirely with the nucleus of protozoa and its significance as the forerunner of the nucleus of the metazoa. Botanists working with the nucleus in the lower algae and fungi, and especially with flagellates, cannot afford to overlook this paper.—CHARLES J. CHAMBERLAIN.

Symbolae Antillanae.[6]—In continuation of this important work Professor URBAN in cooperation with several eminent specialists has issued the second and third fascicles of the seventh volume. There are included descriptions of approximately 300 new species, several varieties, and a few new combinations. The following new genera are proposed: *Sarcopilea* of the Urticaceae, *Plethadenia* of the Rutaceae, *Hypocoton* of the Euphorbiaceae, *Ottoschulzia* of the Icacinaceae, *Maga* of the Malvaceae, *Poicillopsis* of the Asclepiadaceae, *Tuerckheimocharis* of the Scrophulariaceae, and *Shaferocharis* of the Rubiaceae.—J. M. GREENMAN.

NOTES FOR STUDENTS

Root-tubercles of non-leguminous plants.—In an extremely long and somewhat obscure article, which is not made any clearer by the vague illustrations accompanying it, PEKLO[7] gives an account of his studies of the organisms in the root-tubercles of *Alnus* and *Myrica*. With respect to the morphology of the organisms the author adds nothing to what is known from earlier accounts, especially the excellent account of SHIBATA with which he agrees in all essential details. PEKLO finds in the cells of the root-swellings of *Alnus* and *Myrica* masses of filaments with more or less radial arrangement and termi-

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[5] HARTMAN, MAX, Die Konstitution der Protistenkerne und ihre Bedeutung für die Zellenlehre. 8vo. pp. v+54. *figs. 13.* Jena: Gustav Fischer. 1911.

[6] URBAN, I., Symbolae Antillanae seu fundamenta florae Indiae Occidentalis. Vol. VII, fasc. 2, pp. 161–304, 15 June; fasc. 3, pp. 305–432, 1 October. Leipzig: Fratres Borntraeger. 1912.

[7] PEKLO, J., Die pflanzlichen Aktimonykosen. Centralbl. Bakt. II. 27:451–579. 1910.

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nating in the peculiar vesicles described by BRUNCHORST. Like BRUNCHORST, he regards these vesicles as sporangia and describes the fragmentation of their contents into angular "spores." In the filaments themselves, which finally break up into segments, he finds deeply staining bodies described by SHIBATA, and which resemble the spores of bacteria. These are regarded as endospores, although in his subsequent cultural work he appears to have made no attempt to settle the question of the sporelike nature either of these bodies or of the fragments of the vesicles, by showing that they are capable of germination. In view of SHIBATA'S observation that these bodies as well as the filaments are completely absorbed by the host, it seems that an experimental attempt to determine their true nature would have been worth while, especially since the author seems to have found no difficulty in growing his organisms. The characteristics of the organisms in cultures from both *Alnus* and *Myrica* were similar to those observed in the host cells. The indecisive results of the infection experiments, however, leave some doubt as to whether his cultures contained the causal organisms of the root-galls. From the resemblance of the root-gall fungus of *Alnus* and *Myrica* to the animal parasite *Actinomyces*, PEKLO, following a suggestion made by SHIBATA in regard to the fungus of *Myrica*, transfers these organisms to the genus *Actinomyces*, and rebrands the galls, *Actinomycoses*. All these organisms he believes are highly organized bacteria.

BOTTOMLY[8] studying the root nodules of *Myrica Gale* finds that the bulk of the cortical tissue back of the meristem of the growing apex of the young nodules is infected with bacteria. These are massed together in "infection threads" extending from cell to cell. The bacteria were obtained in pure cultures where they showed the characteristics of *Pseudomonas radicicola*. Cultures grown for seven days at 25° C. showed a fixation of 2.05 mg. nitrogen per 100 cc. It was found that *Myrica* plants growing in sterilized soil deficient in nitrogen did not flourish unless they possessed root nodules. When plants free from root nodules and growing poorly were watered with a culture of the bacteria, nodules developed and the plants began to thrive. Fungus filaments are found in the older parts of the galls, sometimes close to the bacteria-infected cells, but although not denying the possible mycorhizal nature of these filaments which are the organisms described by previous investigators, he believes that they have nothing to do with the origin of the nodules or with nitrogen fixation.

Miss SPRATT[9] confirms former observations of BOTTOMLY, according to which the root-gall organisms of *Alnus* and *Elaeagnus* is a bacterium identical with *Pseudomonas radicicola*. The organism occupies the young cortical tissues

[8] BOTTOMLY, W. B., The root nodules of *Myrica Gale*. Ann. Botany **26**: 111–117. 1912.

[9] SPRATT, ETHEL ROSE, The morphology of the root tubercles of *Alnus* and *Elaeagnus*, and the polymorphism of the organism causing their formation. Ann. Botany **26**: 119–128. 1912.

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in a manner similar to that of the organism of *Myrica* described above. Miss SPRATT also finds that under certain conditions, both in the root and in cultures, the organism gives rise to relatively large spherical bodies or coccus forms. This polymorphism seems to be the result of lack of nutrition. When nutriment is supplied they divide and become transformed into typical bacilli. It was also shown that the organisms from both plants were capable of fixing free nitrogen, thus confirming HILTNER'S observations.—H. HASSELBRING.

Morphology of orchids.—VERMOESEN[10] has made a careful study of the development of the ovule in several orchids. He finds arising at the lines of fusion of the three carpels three longitudinal "primary placental protuberances," each of which is caused by the enlargement of a band of subepidermal tissue, usually appearing in cross-section as three cells (possibly from a single one). The lateral members of this band of cells continue to divide actively, while in the median line growth is retarded, resulting in a bifurcation of the placental protuberance. Growth is further checked at various transverse levels, so that the ovary wall soon shows three double rows of small prominences, each with its isolated group of active subepidermal cells. These prominences now branch repeatedly to form the numerous ovulary filaments, each of which finally produces an ovule at its summit. All the steps of this process are initiated by the activity of the subepidermal cells, which retain the characters of archesporial tissue.

The author's main conclusion is that the primary archesporial cells are those which give rise to the original placental protuberance on the wall of the ovary, since this group of cells by repeated dichotomy gives rise to all the tissue within the branched placenta, funiculus, and nucellus. The sterilization idea is extended to include all these organs. It is further held that each carpel originally produced on its ventral surface two marginal archesporial bands which have become fused with those of the neighboring carpels.

The development of an eight-nucleate embryo sac from one megaspore of an "incomplete tetrad" and fertilization occur in the usual manner.—LESTER W. SHARP.

Dioecism in Epigaea.—The flowers of *Epigaea repens* were divided by GRAY into two main groups: one with well developed stigmas and abortive stamens, and the other with small, poorly formed stigmas and well developed stamens. Both groups possess equally good ovaries and ovules, and both show stamens and pistils of various lengths. STEVENS[11] has undertaken to determine two points: (1) whether there is any real evidence of a heterostylic condition, and (2) whether the species is actually dioecious. He finds that

[10] VERMOESEN, CAMILLE, Contribution à l'étude de l'ovule, du sac embryonnaire, et de la fécondation dans les angiospermes. La Cellule **27**:115–162. *pls. 2.* 1911.

[11] STEVENS, NEIL E., Dioecism in the trailing arbutus, with notes on the morphology of the seed. Bull. Torr. Bot. Club. **38**:531–543. *figs. 4.* 1911.

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pollen from stamens of all lengths develops readily on the stigmas of all lengths of pistil, provided the stigmas are of the well formed sort. From this and anatomical evidence he concludes that *Epigaea* is not truly heterostylous. With regard to dioecism, it was found that pollen develops readily upon the well formed stigmas, but not at all upon the poorly formed sort, although ovules with normal embryo sacs are present in the ovaries. Thus the flowers with small stigmas are apparently perfect but are functionally male, and the species is functionally dioecious. The author has also recorded some interesting facts concerning the development of the seed. The embryo sac is of the usual eight-nucleate type, and is surrounded by a layer of "tapetum" except at the much prolonged micropylar end. There is no period of free nuclear division in the development of the endosperm, transverse walls at once separating the sac into four chambers, in all of which the further cells divisions occur rapidly. When the endosperm is well developed it produces at each end a knoblike haustorial outgrowth which extends into the tissue of the integument. —LESTER W. SHARP.

Crown-gall.—In their account of the crown-gall of plants, SMITH, BROWN, and TOWNSEND[12] described the occurrence of secondary galls originating at some distance from primary galls which had been produced by direct infection, and suggested that the secondary galls arose in some way from the primary galls, although the mode of origin was not clear at that time. This problem has now been solved by a histological study of the crown-gall by SMITH, BROWN, and MCCULLOCH.[13] They find that the secondary galls arise from strands of tissue which originate from the primary galls and make their way along the stem or leaf, usually in the region of the primary wood. The tumor strand apparently does not absorb the cells in its path, but makes its way by crushing and flattening them. Secondary galls arise at various points along the tumor strand. A cross-section of a secondary gall developing in the leaf from a strand arising from a primary gall in the stem shows a stem structure with the woody elements greatly developed and regularly arranged like the secondary wood of a stem. If, however, a primary gall develops in the leaf as a result of direct inoculation, its structure is irregular. The tissue consists of an enormous development of parenchyma intermixed with irregular masses of tracheids. There is no distinct differentiation of parts as in the secondary galls arising from stem galls. The similarity which has been formerly pointed out between these plant galls and animal tumors leads the writers to consider the crown-gall apart from all other plant diseases, and to place it in the category of true tumors.—H. HASSELBRING.

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[12] Rev. BOT. GAZ. 52:75. 1911.

[13] SMITH, ERWIN F., BROWN, NELLIE E., and MCCULLOCH, LUCIA, The structure and development of crown gall; a plant cancer. Bur. Pl. Ind. Bull. 255. pp. 60. *figs. 2. pls. 109.* 1912.

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Comparative anatomy of stomata.—From an examination of over 30 species of seed plants, taken from widely scattered genera, WARNCKE[14] finds upon many very divergent forms of stomata upon the different organs. So marked is the diversity that in some instances each organ seemed to possess its own particular type. On the whole, however, stomata on stems and petioles are much alike and are usually larger and with thicker walls than those of foliage leaves. The most divergent forms are those occurring upon rhizomes and in the epidermis of the inner side of sheaths. The very different external conditions will at least partially account for the greater amount of submergence below the level of the epidermis, for the thicker cell walls of the stomata of more exposed organs, and for the tendency toward loss of function and suppression upon the submerged and subterranean parts, but it is quite inadequate to explain the occurrence of two such entirely diverse types as those found upon the outer and inner surfaces of the sheath of *Zea Mays*. As might be expected, a close relationship is found to exist between the type of stomata and the general outline of the epidermal cells.

No phylogenetic sequence is revealed in the various forms examined; indeed, the investigator does not believe that PORSCH[15] is warranted in his conclusions regarding the phylogenetic importance of the types of stomata, since he compared as homologous the stomata of various organs now found to differ to a marked degree upon the same individual, and even, in a few instances, upon different parts of the same organ.—GEO. D. FULLER.

Embryo sac of Crassulaceae.—In 1908 WENT described the ovule and embryo sac of the Podostemaceae, in which he found among other peculiarities an empty cavity or "Pseudoembryosack" extending from the base of the short sac to the chalazal region. This has led Miss ROMBACH[16] to investigate the related Crassulaceae in the hope of throwing some light upon the significance of this peculiarity. Eight species were examined, which showed agreement in all essential features. A subepidermal cell of the very reduced nucellus cuts off one parietal cell and then divides to form four megaspores, the innermost of which gives rise to an embryo sac of the ordinary eight-nucleate type. During the early development of the endosperm and embryo the base of the sac with the antipodals grows downward through a central strand of loose, elongated cells until it reaches the chalaza.

The author believes that here are present side by side two processes: the outgrowth of the embryo sac, and cavity formation by the nucellus. In the Podostemaceae it is supposed that the embryo sac formerly filled all the

[14] WARNCKE, FREDERICK, Neue Beiträge zur Kenntnis der Spaltöffungen. Jahrb. Wiss. Bot. **50**: 21–66. 1911.

[15] PORSCH, O., Der Spaltöffungsapparat im Lichte der Phylogenie. Jena. 1905.

[16] ROMBACH, SARA, Die Entwicklung der Samenknospe bei den Crassulaceen. Rec. Trav. Bot. Neerlandais **8**: 182–200. *figs. 10.* 1911.

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cavity down to the chalaza, as in the Rosaceae, but for some reason, possibly as a result of the peculiar mode of life shown by these plants, the outgrowth process no longer occurs, so that the empty "Pseudoembryosack" remains. The Crassulaceae are thus regarded as transitional forms between the Podostemaceae and the Rosaceae.—LESTER W. SHARP.

Antarctic lichens.—In 1909 DARBISHIRE[17] reported on the very extensive collection of lichens secured by the Norwegian polar expedition of 1898–1902 under NANSEN. In connection with this report it was shown that from the region including Arctic America, Greenland, Spitzbergen, and Iceland about 500 lichens have been recorded. A similar report has now been published by DARBISHIRE[18] for the antarctic region, based upon the collection brought back by the Swedish antarctic expedition of 1901–1903. There are now known 534 lichens from the general antarctics (subantarctic America, South Georgia, and the true antarctic region), 145 of which were secured by the expedition, 34 of them being new species. The true antarctic region contains 106 known lichens. It is an interesting fact that the relation of arctic to alpine lichens is much greater than that of subantarctic American species to those of New Zealand. It is further obvious that the similarity of subantarctic to arctic species is less striking than that of antarctic to arctic species, 43 per cent of the antarctic lichens being found in the true arctics and not in temperate regions.

The new species are distributed among 17 genera, *Lecidia* and *Buellia* having 5 each; *Pertusaria*, *Aspicilia*, and *Verrucaria* having 3 each; *Bacidia*, *Lecanora*, and *Parmeliella* having 2 each. The remaining genera, each represented by one new species, are *Biatora*, *Thelotrema*, *Placodium*, *Caloplaca*, *Pannoparmelia*, *Parmelia*, *Rinodina*, *Acarospora*, and *Chaetomium*.—J. M. C.

A new Williamsonia.—SEWARD[19] has studied petrified material of a *Williamsonia* from the Jurassic of Scotland, to which he gives the name *W. scotica*. It proves to be an exceedingly interesting and suggestive form. The most striking vegetative feature is the replacement of the usual scales (ramentum) of the Bennettitales by an abundance of very long hairs, such as occur on *Dioon edule* and other living cycads. The sections of the strobilus, the first obtained of a *Williamsonia*, are of special interest. The bisporangiate character is problematical, since no stamens were evident and NATHORST has shown that some species of *Williamsonia* were monosporangiate.

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[17] DARBISHIRE, OTTO V., Lichens collected during the second Norwegian polar expedition in 1898–1902. Publ. Soc. Arts and Sciences Kristiania. 1909.

[18] ———, The lichens of the Swedish antarctic expedition. Wiss. Ergebn. Schwed. Südpolar-Exped. 1901–1903. **4**: no. 11 (pp. 73). *pls. 3.* 1912.

[19] SEWARD, A. C., A petrified *Williamsonia* from Scotland. Phil. Trans. Roy. Soc. London B **203**: 101–126

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The interseminal scales and megasporophylls (stalks bearing terminal ovules), however, are of the *Bennettites* type, but much simpler in structure, although some of the simplicity may be due to immaturity.

It is refreshing to obtain the following statement from an English paleobotanist: "The morphology of the Bennettitean flower is still a problem to be solved, and the attractive hypothesis that would have us regard this dominant group of the Mesozoic era as a guide to the evolution of the class which now occupies the pre-eminent position in the vegetable kingdom, requires to be substantially strengthened before it can claim to have solved the mystery of the origin of the flowering plants."—J. M. C.

Cytology of seedless oranges.—OSAWA[20] has investigated the cytological situation in the two seedless oranges known as the "Washington navel" (*Citrus aurantium*) and the "Unshu" (*C. nobilis*), chiefly using *C. trifoliata* as a check species. After showing that spermatogenesis and oogenesis in *C. trifoliata* are as usual among angiosperms, he finds in both the seedless forms a strong tendency toward the disorganization of pollen mother cells and megaspores. In the "Unshu" there is every stage in the failure of pollen development from a failure in the differentiation of sporogenous tissue up to the reduction divisions. In the majority of cases, however, pollen grains are produced. In the "Washington navel," spermatogenesis in the majority of cases does not proceed beyond the mother cell stage. In both forms oogenesis usually proceeds to the formation of megaspores and then fails. As some normal embryo sacs are produced a few seeds were obtained; and the usual failure of seeds is due chiefly to the failure of embryo sacs rather than of pollen grains, especially in the case of the "Unshu." The chromosome numbers in this form are 8 and 16. In *C. trifoliata* it was discovered that fertilization occurs about four weeks after pollination, and the fertilized egg divides three or four weeks after fertilization.—J. M. C.

Pine-barrens of New Jersey.—A careful examination of geological evidence leads TAYLOR[21] to the conclusion that the pine-barrens of New Jersey coincide in distribution with the geological Beacon Hill formation, an area that has been uninterruptedly out of the water since the Upper Miocene, and has several times been more or less completely surrounded by water. This would make this plant formation by far the oldest in New Jersey. Its xerophytic character does not appear to harmonize well with such a theory, although the number of more or less endemic species would seem to demand a rather complete and extended period of isolation such as the submergence and glaciation

[20] OSAWA, I., Cytological and experimental studies in *Citrus*. Jour. Coll. Agric. Tokyo **4**:83–116. *fig. 1. pls. 8–12.* 1912.

[21] TAYLOR, NORMAN, On the origin and present distribution of the pine-barrens of New Jersey. Torreya **12**:229–242. 1912.

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of adjacent territory would afford. The evidence offered of the large proportion of non-autophytic plants included in the pine-barren flora would tend to indicate a plant formation of considerable antiquity. The species from the far north in the pine-barrens are explained as having come down with the advancing ice sheets and having become isolated in bogs such as were probably to be found within the area in question during the glacial period. This evidence seems to add probability to the hypothesis, which seems to be the best yet offered in explanation of the peculiar flora of this interesting plant formation. —GEO. D. FULLER.

Origin of maize.—COLLINS[22] has been attacking the problem of the origin of maize by extensive cultures of the different types of maize, teosinte (*Euchlaena mexicana*), and teosinte-maize hybrids, through a period of seven years. The current view is that maize was derived from its nearest wild relative, teosinte. COLLINS concludes that it originated as a hybrid between teosinte and an unknown grass belonging to the Andropogoneae, a grass which resembled the earless varieties of pod corn (*Zea tunicata*). In enumerating the pronounced differences between teosinte and pod corn, he calls attention to the fact that in practically every case the characters of maize are intermediate. The origin of the maize "ear" has always been an interesting question. COLLINS regards it as the homologue of the central spike of the staminate inflorescence, but the central spike is quite as anomalous as the ear, and to account for it may call for the fasciation of simple branches of the inflorescence. In this sense, therefore, both opinions as to the nature of the maize ear (central spike or fasciation) may be right.—J. M. C.

Influence of adult on seedling.—HILL and DEFRAINE[23] have investigated the seedling structure of *Persoonia lanceolata* (Proteaceae) as a basis for the claim that the adult structure influences that of the seedling. The occurrence of polycotyledony among the Proteaceae is well known, and also the resemblance in the habit of some of them to the gymnosperms. The number of cotyledons in *P. lanceolata* ranges from three to five, and the authors are convinced that they have arisen by the splitting of two original structures. The details of the seedling structure further emphasize the close resemblance to the polycotyledonous gymnosperms, "a resemblance which is found not only in the general morphological configuration, but also in certain histological details and in the transition phenomena." The authors, of course, attach no phylogenetic significance to these similarities, but "the resemblance is considered as a striking instance of homoplasy in which the adult has influenced to a considerable extent the seedling."—J. M. C.

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[22] COLLINS, G. N., The origin of maize. Jour. Wash. Acad. Sci. 2:520–530. 1912.

[23] HILL, T. G., and DEFRAINE, E., On the influence of the structure of the adult plant upon the seedling. New Phytol. 11:319–332. *figs. 9.* 1912.

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Vascular anatomy of Ophioglossaceae.—LANG[24] has been investigating the vascular anatomy of the three genera of Ophioglossaceae, and in advance of the publication of the full papers he has made a brief statement of his conclusions. It is becoming increasingly evident that the Ophioglossaceae are true ferns, and this return to the earlier views as to their relationships is emphasized by the present paper. The critical study of the anatomy of the stem and leaf trace led to the conclusion that there is "an essential similarity in plan of stelar construction between the Ophioglossaceae and the Coenopterideae" (Botryopterideae and Zygopterideae). There are also features in common with the Osmundaceae and Hymenophyllaceae. When one considers the gaps in our knowledge of the extinct forms, it is safer to suggest relationship in a general way than to be too specific, and this attitude LANG has taken. He is convinced, further, that in the Ophioglossaceae a protostele has developed intrastelar pith.—J. M. C.

Vegetative reproduction in Angiopteris.—It has been known for a long time that the leaf stalk of *Angiopteris* is differentiated into two regions, a basal portion bearing stipules, and a midrib bearing pinnae, the two regions being separated by an abscission layer. From material in the garden and from a study of large specimens in the forest, VAN LEEUWEN[25] records the following observations: the foliage leaf persists for about two or three years and then breaks off at the abscission layer, the leaf base remaining many years longer; after the leaf has fallen, four resting buds appear on the leaf base, and when it finally falls off, one or more of the buds begin to grow and many develop into new plants.

RACIBORSKI first noticed such buds in *Angiopteris;* the present account gives additional information from plants growing under natural conditions.—CHARLES J. CHAMBERLAIN.

Fossil prothallia.—MCLEAN[26] has added to our meager knowledge of paleozoic prothallia by describing two female prothallia from the Lower Coal Measures of England. One is that of the classic *Lagenostoma Lomaxii*, and it resembles closely the female gametophyte of modern gymnosperms, the radial arrangement of the tissues suggesting centripetal growth by "alveoli." This radial arrangement is lacking in such a gametophyte as that of *Lepidocarpon*. The other gametophyte is that of *Bothrodendron*, one of the lycopods. It is extremely well preserved, and strongly resembles the emergent and

[24] LANG, WILLIAM H., On the interpretation of the vascular anatomy of the Ophioglossaceae. Mem. and Proc. Manchester Lit. and Phil. Soc. **56**: no. 12 (pp. 14). *figs. 6.* 1912.

[25] VAN LEEUWEN, W. DOCTERS, Über die vegetative Vermehrung von *Angiopteris evecta* Hoffm. Ann. Jard. Bot. Buitenzorg **10**: 202–209. *pl. 18.* 1912.

[26] MCLEAN, R. C., Two fossil prothalli from the Lower Coal Measures. New Phytol. **11**: 305–318. *figs. 2. pls. 5, 6.* 1912.

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flaring gametophyte of the water ferns, with the archegonia developed outside the spore. Since the female gametophyte of *Lepidocarpon* remains entirely within the megaspore, that of *Bothrodendron* represents a more primitive condition, in which the gametophyte is partly free from its spore.—J. M. C.

Cold air drainage.—In investigating the physical factors influencing the distribution of vegetation in the Santa Catalina Mountains, SHREVE[27] has found important differences in the temperature limits of stations at similar altitudes, but differently related to the ridges and valleys of the mountain slopes. These differences are shown to be due to valleys and cañons being frequently occupied by a stream of cooled air, and to amount to a difference in the mean minimum temperature equivalent to that usually experienced with an increase in altitude of 2350 feet. The influence of this cold air drainage seems to be most important in its effect upon the upward distribution of lowland species, and will do much to account for the higher range of these species upon the ridges and upper slopes of cañons.—GEO. D. FULLER.

Botryopterideae.—LIGNIER[28] has investigated *Stauropteris Oldhamia*, and its relations to the Botryopterideae, which he prefers to call Coenopterideae. Following the theory of the meriphyte, and including the sporangial structures, he reaches the conclusion that *Stauropteris* does not belong to the Coenopterideae, which represent an advanced group, but very near to the more primitive Primofilices. Incidentally he presents a "genealogical tree," which indicates that the Primofilices have given rise to three lines: (1) to the Coenopterideae (Botryopterideae) through *Stauropteris* as a start; (2) to the Marattiaceae through *Archaeopteris* and *Botrychium*, with a possible side branch leading to the Leptosporangiates; (3) to the Pteridosperms (Cycadofilicales).—J. M. C.

Standardizing atmometers.—The difficulties involved in subjecting a considerable number of atmometer cups to exactly similar conditions of temperature, humidity, and air movement for the period of time necessary for their standardization has caused LIVINGSTON[29] to devise a table rotating once per minute by means of a small electric motor belted to a reducing gear. The cups, mounted in suitable bottles, are placed near the outer margin of the table, and should a very high rate of evaporation be required an electric fan is made to furnish a current of air crossing the table. As the efficiency of the atmometer is largely dependent upon the accuracy of its standardization this device will prove helpful to ecological workers.—GEO. D. FULLER.

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[27] SHREVE, FORREST, Cold air drainage. Plant World **15**:110–115. 1912.

[28] LIGNIER, O., Le *Stauropteris Oldhamia* Binney et les Coenoptéridées à la lumière de la théorie du mériphyte. Bull. Soc. Bot. France **59**:1–33. *figs. 11.* 1912.

[29] LIVINGSTON, B. F., A rotating table for standardizing porous cup atmometers. Plant World **15**:157–162. 1912.

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Water relations of plants.—In order to make clear the complex relationships which determine the moisture content of the growing plant and more especially to emphasize the artificial character of the distinction usually made between the organism and its environment, LIVINGSTON[30] has prepared an excellent schematic representation. It should prove a valuable aid to teachers of ecology and plant physiology in presenting this difficult topic. The general theory of physical causation is made to apply to all the organic phenomena involved.—GEO. D. FULLER.

Habitats of the red cedar.—HARPER,[31] in seeking for an explanation for the occurrence of *Juniperus virginiana* in very diverse habitats, finds one which he deems satisfactory in the sensitiveness of the tree to fire. Its prevalence upon limestone soils is noted and the conclusion is reached that "the cedar dreads fire more than it likes lime," and that it is found chiefly in areas which are rarely visited by forest fires. No experimental data are offered in support of this conclusion.—GEO. D. FULLER.

A new Jurassic fern.—THOMAS[32] has described from the Jurassic of England a new species of the *Stachypteris* of POMMEL (1847). In studying the affinities of the genus, he concludes that the structure of the sporangia and of the fertile spikes does not indicate any close affinities with the modern groups of ferns, but that it must belong to "a group of ferns intermediate in their characters between the Cyatheaceae and the Schizaeaceae."—J. M. C.

Embryogeny of Ranunculaceae.—In continuing his studies of the embryo of Ranunculaceae, SOUÈGES[33] has published a detailed account of the embryogeny of *Adonis*. The preceding parts have dealt with the Clematideae[34] and with *Myosurus*.[35] In *Myosurus* the sequence of events is very constant, while in *Adonis* it is very variable.—J. M. C.

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[30] LIVINGSTON, B. E., A schematic representation of the water relations of plants; a pedagogical suggestion. Plant World **15**:214–218. 1912.

[31] HARPER, R. M., The diverse habitats of the eastern red cedar and their interpretation. Torreya **12**:145–154. 1912.

[32] THOMAS, H. HAMSHAW, *Stachypteris Hallei*, a new Jurassic fern. Proc. Cambridge Phil. Soc. **16**:610–614. *pl. 4*. 1912.

[33] SOUÈGES, R., Recherches sur l'embryogénie des Renonculacées. Anémonées (genre *Adonis*). Bull. Soc. Bot. France **59**:474–482, 545–550. *figs. 224–269*. 1912.

[34] BOT GAZ. **51**:480. 1911.

[35] BOT. GAZ. **54**:264. 1912.

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THE EFFECT OF CERTAIN CHLORIDES SINGLY AND COMBINED IN PAIRS ON THE ACTIVITY OF MALT DIASTASE[1]

LON A. HAWKINS

The effects produced by single inorganic salts in aqueous solution upon an organism and the modification of these effects by the presence of other salts has been the subject of considerable research. It has frequently been found that a definitely toxic influence of one salt may be completely removed by the addition of a second salt, itself also markedly toxic when used alone. This mutual counteraction by salts of the toxic influence of each other has been termed antagonism. While single salts and their combinations do not, of course, affect all organisms in the same way, yet different investigators have shown antagonistic salt action in the case of many organisms and with many chemical compounds. Thus, LOEW[2] demonstrated that the injurious action of certain concentrations of magnesium nitrate upon *Spirogyra majuscula* is inhibited by the presence in the medium of a proper amount of calcium nitrate. Similarly LOEB[3] found an antagonism to exist between the nitrates of calcium and of sodium in their influence upon the

[1] Botanical contribution from the Johns Hopkins University. No. 23.

[2] LOEW, O., Über die physiologischen Functionen der Calcium- und Magnesium-Salze im Pflanzenorganismus. Flora 75:368–394. 1892.

[3] LOEB, J., Studies on the physiological effects of the valency and possibly the electrical charges of ions. I. The toxic and antitoxic effects of ions as a function of their valency and possibly their electrical charge. Am. Jour. Physiol. 6:411–433. 1902.

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development of the eggs of *Fundulus;* and OSTERHOUT,[4] working with plants, has shown the same kind of antagonism between the salts of magnesium and of potassium. That calcium and potassium influence each other in their effect upon certain bacteria has been brought out by LIPMAN.[5]

In a theoretical consideration of the possible causes of chemical stimulation, it is suggested that, since many vital phenomena seem to be dependent upon enzymes, it is possible that the influence of chemical substances upon the activity of plants and animals may be due in some measure to the action of such substances in accelerating or retarding enzyme activity. With these ideas in mind, it was undertaken to study the relation between the catalytic action of some enzyme and the concentration in the medium of certain salts, to determine, if possible, whether enzyme catalysis is influenced independently by two salts simultaneously present in the medium, or whether either salt increases or decreases the accelerating or retarding influence of the other upon such catalytic reactions.

The studies here reported bear upon this question and were carried out in part in the new Laboratory of Plant Physiology of the Johns Hopkins University, at Homewood, and in part in the Biological Laboratory of the Johns Hopkins University. The writer is greatly indebted to Professor BURTON E. LIVINGSTON, under whom this investigation was conducted, for his many helpful suggestions and criticisms.

Materials

The enzyme chosen for investigation was, for practical reasons, malt diastase (Merck's "diastase of malt absolute"), and the salts used were chlorides of sodium, potassium, calcium, magnesium, copper, and iron (Kahlbaum's "chemically pure" salts were exclusively used). The activity of the diastase was measured in terms of the length of time required for it to render a starch paste (of washed maize starch) powerless to give color reactions with iodine.

[4] OSTERHOUT, W. J. V., The antagonistic action of magnesium and potassium. BOT. GAZ. 45:117–124. 1908.

[5] LIPMAN, CHARLES B., Toxic and antagonistic effects of salts as related to ammonification by *Bacillus subtilis*. BOT. GAZ. 48:105–125. 1909.

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All water used was distilled from glass and condensed in a well seasoned glass condenser. The various pieces of apparatus coming in contact with the solutions or mixtures of the experiments were carefully cleansed in this water before use.

Method

The method here employed for determining the duration of hydrolysis is similar to that described by SHERMAN, KENDALL, and CLARK as the liquefaction method for estimating diastatic activity.[6] The exact procedure in the present study was as follows: A sufficient quantity of starch for the entire study was purchased at one time and thoroughly mixed. Of this material 2.5 grams were weighed out, placed in a porcelain dish, and by means of a glass rod rubbed into a suspension with a little water. This mixture was then diluted to a volume of 500 cc., boiled two minutes, and then strained through cheesecloth, thus making a 0.5 per cent starch paste, a homogenous liquid which flows freely and is easily measured from a burette.

With the exception of a small amount used in preliminary tests, all the diastase for the investigation was purchased at one time and thoroughly mixed to insure uniformity. It was preserved in a glass-stoppered bottle and showed no signs of deterioration during the several months the study was in progress. A 2 per cent solution of this diastase was prepared in much the same manner as that employed in making the starch paste. Two grams of the dry material were first thoroughly suspended in a small amount of water and then diluted to a volume of 100 cc., after which the solution was filtered. Fresh diastase solution and also fresh starch paste were prepared at the beginning of each experiment, to preclude the possibility of error resulting from the growth of microorganisms. No antiseptic was used in the various mixtures.

Stock salt solutions, sufficient in quantity for the entire study, were prepared at the beginning of the investigation, in concentrations of 1–4 gram molecules per liter of solution, and from these the requisite dilutions were made. The iodine solution used in the tests was originally prepared in quantity sufficient for the whole

[6] SHERMAN, H. C., KENDALL, E. C., and CLARK, E. D., Studies on amylases. I. An examination of methods for the determination of diastatic power. Jour. Am. Chem. Soc. 32: 1073–1087. 1910; references to the earlier literature are given here.

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research in a concentration of 1.5 grams of iodine and 3 grams of potassium iodide per liter of water.

In experimentation the various mixtures were placed in large test tubes (30 mm. in diameter and 150 mm. deep), which were suspended through the suitably perforated top of a cylindrical water-bath. The water of the bath stood always at a higher level than that of the liquid in the tubes, which were some distance apart, the outer ones being several centimeters from the walls of the bath. It was thus assured that the mixtures in the tubes were maintained at the same temperature as the surrounding water. The temperature of the bath was kept nearly constant at 50° C., by means of an ordinary mercury regulator and a gas flame below. The variations in temperature were between the limits of 48° and 52°. Since the computations of the velocity of diastatic activity were always made in terms of the velocity of the reaction in controls within the same series, the possible effects of temperature fluctuations should be exceedingly slight.

A series of mixtures was usually prepared in the following manner: In each of a series of tubes was placed the proper amount of salt solution at a concentration in each case of four times[7] the required concentration for each particular tube. To this were added 5 cc. of water, in the cases where the action of a single salt was to be tested, or an equal quantity of the solution of the other salt, in those where salt combinations were to be used; 8 cc. of starch paste (0.5 per cent) were then added to each tube, followed by 2 cc. of the previously prepared diastase solution. The tubes, containing 20 cc. of mixture, were immediately placed in the water-bath. It is thus apparent that all test mixtures contained the same quantity (0.2 per cent or 0.004 gm.) of the starch and of the diastase.

An experiment was usually made up of (1) a series of 7 different concentrations of some salt used singly; (2) a series of 7 different concentrations of another salt used singly, and (3) a series, usually in duplicate, of the 7 concentrations of the two salts in binary combinations. These with the two control tubes made a total of

[7] For 2m mixtures 10 cc. of the 4m stock salt solution were placed in each tube; this when diluted to 20 cc. by the addition of the starch and diastase gave the required concentration of the salt.

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30 tubes to be tested at one time. The control tubes were prepared in exactly the same way as the others, except that water was substituted for the salt solution. In order to determine whether or not the salt solutions alone had any appreciable hydrolytic effect upon the starch, tubes were frequently made up with the salt solution and starch content the same as those in the experiment but without the diastase. These were placed in the water-bath together with the other tubes and tested from time to time in the usual manner, but in no case was there any variation from the typical blue color of the starch-iodine reaction. It was thus clear, as was to be expected, that while the salts could influence the velocity of the action of the diastase on starch, they were themselves apparently incapable of any appreciable hydrolytic action.

To determine whether the contents of any given tube had reached the end point, a single drop of the stock iodine solution was placed in each of two small vials (10 mm. in diameter and 70 mm. high). To one vial was added 1 cc. of water and to the other a like quantity of the mixture from the proper tube, carefully pipetted out. The two vials were then observed against a white background in diffused light, and if their contents appeared to be of the same color (a pale yellow) the experimental end point was considered to have been attained. It has been found that by this method of determining the end point, the color produced in a starch paste containing but 0.0002 of 1 per cent can be readily detected. This sensitiveness lies well within the limits of error of the other operations of the experiments. Final failure of one of the starch-diastase mixtures to produce color (blue, purple, red, brown, etc.) does not necessarily mean that all of the original starch content has been converted into a reducing sugar, but merely that all of the starch has been so altered as to be no longer able to form colored compounds with iodine—showing that one or several of the steps of the process of hydrolysis have been completed. In this connection it may be remarked that LANG[8] has shown with pancreatic amylase that the amount of a reducing sugar present at the time when the starch paste first fails to color with iodine does not represent and

[8] LANG, S., Über die Einwirkungen der Pankreasdiastase auf Stärkearten verschiedenen Herkunft. Zeitschr. Exper. Path. u. Therapie 8:279–307. 1910.

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is not proportional to the original amount of starch. The present investigation is therefore not directly comparable with such investigations as those of KJELDAHL,[9] KELLERMAN,[10] MCGUIGAN,[11] and others, who measured diastatic activity by determining the amount of a reducing sugar formed in a given time. For a more complete bibliography on the effects of salts on diastatic action, the reader is referred to EFFRONT,[12] GREEN,[13] OPPENHEIMER,[14] EULER,[15] as well as to the literature cited here.

Experimentation

The water, diastase, and starch used in this work were tested for neutrality in the course of the investigation, and it was found that while the water and starch-paste were neutral to phenolphthalein, the diastase solution was strongly acid, requiring 1.2 cc. of 0.01 normal hydrate to neutralize 2 cc. of the stock solution. Thus each tube of mixture as actually used possessed an acidity equivalent to 1/1660, or 0.000602 normal. Several series were carried out by neutralizing or partially neutralizing (with sodium hydrate) this acidity of the diastase, and a strong retardation was evident when even a small quantity of the alkali was added. Thus the use of 5 cc. of 0.0005 alkali diluted to 20 cc. by the addition of the usual amounts of diastase solution, starch-paste, and water (reducing the acidity of the mixture to 0.000477 normal) caused a retardation of 13 per cent as compared with the control without the alkali. With a further decrease in the acidity to 0.000352 normal, there was apparently but little action of the diastase, and when the original acidity was completely neutralized,

[9] KJELDAHL, Recherches sur les ferments producteurs de sucre. Compt. Rend. Lab. Carlsberg 1:109–157. 1879.

[10] KELLERMAN, KARL F., The effects of various chemical agents upon the starch-converting power of taka diastase. Bull. Torr. Bot. Club 30:56–70. 1903.

[11] MCGUIGAN, H., The relation between the decomposition-tension of salts and their antifermentative properties. Am. Jour. Physiol. 10:444–451. 1904.

[12] EFFRONT, JEAN, Enzymes and their applications. (PRESCOTT's trans.) New York. 1902.

[13] GREEN, J. REYNOLDS, The soluble ferments and fermentation. Cambridge University Press. 1901.

[14] OPPENHEIMER, KARL, Die Fermente und ihre Wirkungen. Leipzig. 1910.

[15] EULER, HANS, Allgemeine Chemie der Enzyme. Wiesbaden. 1910.

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no alteration in the starch could be detected by the iodine test, after a period of 5 hours in the water-bath.

A determination of the resistances of the starch and diastase solutions by means of a Wheatstone bridge and the calculation of corresponding conductivities showed the presence of a small quantity of electrolytes in the mixture. These must have modified to some extent the effect of the addition of the different salts in the experiments. Since, however, the same concentrations of starch and diastase were employed throughout the investigation, the electrolytes originally present are to be considered as constant in quantity. Furthermore, the concentrations of the salts used were usually comparatively high, so that any resulting errors due to what may be termed electrolytes of impurity (or of constitution) of the mixture used must be relatively slight.

It was observed in many cases that, in mixtures containing salts at the higher concentrations used, a flocculent precipitate was gradually formed during the experiment. This precipitate was isolated and gave no starch reaction with iodine. No relation could be detected between its occurrence or amount and the diastatic activity. It seems, therefore, that the effect of the presence of a salt in increasing or decreasing diastatic activity cannot be due to a salting out from the solution of either diastase or starch. This is in accord with the conclusion reached by COLE[16] in his work on ptyalin, but contrary to what might seem to be the case from the investigations of HARDY.[17] In this connection it is interesting to note that MUNTER[18] has recently shown that many of the salts of the alkalies and alkaline earths are ineffective for the precipitation of the diastase of *Aspergillus oryzae*.

Testing was begun when the mixtures had remained in the water-bath one hour, and was continued thereafter at intervals of 15 minutes until the conclusion of the experiment. Thirty or more

[16] COLE, S. W., Contributions to our knowledge of the action of enzymes. Part I. The influence of electrolytes on the action of amylolytic ferments. Jour. Physiol. **30**:202–220. 1903.

[17] HARDY, W. B., A preliminary investigation of the conditions which determine the stability of irreversible hydrosols. Proc. Roy. Soc. London **66**:110–125. 1900.

[18] MUNTER, F., Über Enzyme. Landwirtsch. Jahrb. Erganzband III. **39**:298–314. 1910.

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similar vials were prepared before each test, each with its drop of iodine solution, and the samples were consecutively pipetted into these from the tubes, following the order in which the diastase had been originally added. The pipette was thoroughly washed after each use and thoroughly clean vials were always employed.

The number of minutes which elapsed before the end point was reached for each mixture was recorded, thus furnishing a means for the quantitative comparison of the enzyme activity under the different conditions. For example, a series of 2, 1/2, 1/8, 1/32, 1/128, 1/512, and 1/2048 molecular sodium chloride gave for the respective

TABLE I

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF SODIUM AND POTASSIUM CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions 1:1)	
NaCl		KCl			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
2m	1.51	2m	1.77	4m	....
m/2	1.71	m/2	2.19	Mol.	1.38
m/8	1.82	m/8	1.61	m/4	1.93
m/32	1.42	m/32	1.39	m/16	1.92
m/128	0.85	m/128	0.85	m/64	1.07
m/512	0.95	m/512	0.93	m/256	0.89
m/2048	1.02	m/2048	1.00	m/1024	0.96

time periods 165, 165, 150, 180, 315, 285, and 300 minutes, the control mixture (without any added salt) reaching the end point in 285 minutes.[19] The intensity of the enzyme action in experiments such as these is, of course, for any given mixture reciprocally proportional to the number of minutes required for that mixture to reach the end point. Thus the ratio of the time period of the control to that of any mixture is obviously a measure of the velocity of the hydrolysis for that mixture in terms of the velocity of the control. Thus, the relative velocities or intensities of starch hydrolysis for the experiment just cited become, respectively, 285/165,

[19] The time periods for the two control tubes were the same in all series except three, and in these cases the two results (differing but slightly) have been averaged.

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285/165, 285/150, 285/180, 285/315, 285/285, and 285/300, or 1.73, 1.73, 1.90, 1.58, 0.90, 1.00, and 0.95, when the velocity of the reaction without added salt is taken as unity.

TABLE II

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF SODIUM AND CALCIUM CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions, NaCl 2:$CaCl_2$ 1)	
NaCl		$CaCl_2$			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
2m	1.51	Mol.	Retardation	3m	Retardation
m/2	1.71	m/4	1.33	3m/4	1.21
m/8	1.82	m/16	2.89	3m/16	3.29
m/32	1.42	m/64	3.69	3m/64	3.40
m/128	0.85	m/256	3.01	3m/256	2.75
m/512	0.95	m/1024	1.88	3m/1024	1.85
m/2048	1.03	m/4096	1.07	3m/4096	1.17

TABLE III

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF SODIUM AND MAGNESIUM CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions, NaCl 4:$MgCl_2$ 1)	
NaCl		$MgCl_2$			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
2m	1.51	m/2	Retardation	5m/2	Retardation
m/2	1.71	m/8	2.25	5m/8	0.98
m/8	1.82	m/32	2.07	5m/32	1.90
m/32	1.42	m/128	1.97	5m/128	2.21
m/128	0.85	m/512	1.35	5m/512	1.54
m/512	0.95	m/2048	1.07	5m/2048	0.89
m/2048	1.02	m/8192	1.00	5m/8192	0.99

These numbers may be termed the ratios of the enzyme activity or of efficiency. Such a computation as the foregoing has been made in each case, always with the enzyme activity of the control for the particular experiment in question taken as unity, and it

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is with the efficiency ratios for the diastase in the presence of the various concentrations of the different salts that this paper has to deal. These ratios should be comparable throughout the entire

TABLE IV

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF POTASSIUM AND CALCIUM CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions, KCl 2:$CaCl_2$ 1)	
KCl		$CaCl_2$			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
2m	1.77	Mol.	Retardation	3m	Retardation
m/2	2.19	m/4	1.33	3m/4	1.24
m/8	1.61	m/16	2.89	3m/16	2.73
m/32	1.39	m/64	3.69	3m/64	2.87
m/128	0.85	m/256	3.01	3m/256	2.87
m/512	0.93	m/1024	1.88	3m/1024	2.13
m/2048	1.00	m/4096	1.07	3m/4096	1.14

TABLE V

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF POTASSIUM AND MAGNESIUM CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions, KCl 4:$MgCl_2$ 1)	
KCl		$MgCl_2$			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
2m	1.77	m/2	Retardation	5m/2	Retardation
m/2	2.19	m/8	2.25	5m/8	1.07
m/8	1.61	m/32	2.07	5m/32	1.83
m/32	1.39	m/128	1.97	5m/128	2.07
m/128	0.85	m/512	1.35	5m/512	1.20
m/512	0.93	m/2048	1.07	5m/2048	1.12
m/2048	1.00	m/8192	1.00	5m/8192	1.08

study; where they are less than unity the salt or salts have exerted a retarding influence upon hydrolysis; where they equal unity the salt treatment has been without effect; and where they are greater than unity the effect of the salts has been to accelerate the

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action of the enzyme. Of course the combination treatments possess a total salt concentration equal to the sum of the two individual concentrations of the single salts which have been combined.

TABLE VI

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF MAGNESIUM AND CALCIUM CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions, $MgCl_2$ 1 : $CaCl_2$ 2)	
$MgCl_2$		$CaCl_2$			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
m/2	....	Mol.	Retardation	3m/2	Retardation
m/8	2.25	m/4	1.33	3m/8	1.06
m/32	2.07	m/16	2.89	3m/32	3.06
m/128	1.97	m/64	3.69	3m/128	3.61
m/512	1.35	m/256	3.01	3m/512	2.65
m/2048	1.07	m/1024	1.88	3m/2048	2.09
m/8192	1.00	m/4096	1.07	3m/8192	1.16

TABLE VII

EFFICIENCY OF DIASTATIC ACTION AS AFFECTED BY VARIOUS CONCENTRATIONS OF FERRIC AND CUPRIC CHLORIDES, SINGLY AND COMBINED

Single salts				Combinations (Molecular proportions, 1:1)	
$FeCl_3$		$CuCl_2$			
Concentration in mixture	Efficiency	Concentration in mixture	Efficiency	Total salt concentration in mixture	Efficiency
m/1024	Retardation	m/1024	Retardation	m/512	Retardation
m/2048	1.45	m/2048	3.50	m/1024	Retardation
m/4096	3.55	m/4096	2.62	m/2048	3.17
m/8192	3.91	m/8192	1.26	m/4096	3.59
m/16,384	1.98	m/16,384	1.00	m/8192	1.92
m/32,768	1.57	m/32,768	1.00	m/16,384	1.45
m/65,536	1.00	m/65,536	1.00	m/32,768	1.00

The total salt concentrations for the several combinations are given in the tables. It was impracticable to combine 2m NaCl with 2m KCl, so this combination was not tested. The molecular proportions at which any two salts were combined are clear from

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the concentrations of the single salts standing in the same line with the datum for the combination, but these proportions are stated at the head of the columns of combinations. In those cases where the word "retardation" occurs in the efficiency column, this denotes that the efficiency here is much below that of the control without added salt, the end point not having been reached at the close of the experiment in question.

EFFECT OF SINGLE SALTS

From the foregoing tables it is apparent that all the salts used in this investigation, at some concentrations (both singly and in combination), increase the rate of hydrolysis over that of the control without added salt; at certain other concentrations they retard this process; and at still others they have apparently no influence on diastatic activity as measured in this study. Thus, with the chlorides of sodium and potassium, used singly, it may be seen that with a concentration of m/2048 the effect is practically the same as in the control with distilled water. An increase in salt content, however (to m/512), results in a slight retardation of diastatic action; while with a further increase of added salt (to m/128), the point of maximum retardation, as found in this investigation, is attained. All higher concentrations used, of these two salts, accelerate hydrolysis, the points of maximum acceleration being at a concentration of m/8 for sodium chloride and of m/2 for the potassium salt. Possibly the most striking feature of the results shown in table I is that retardation apparently occurs only at relatively low concentrations. To supplement the evidence obtained from the experiments, that there was a retardation with m/128 sodium chloride and potassium chloride as here employed, five additional series were carried out with the two salts singly at this concentration accompanied by the required controls without added salt, all made up and tested in the usual manner. In every case a marked retardation was evident in the mixtures containing the salts, as compared with the controls. This retardation cannot be due to a partial neutralization of the acidity of the diastase by small amounts of free alkali present in the salt solutions (the latter were very slightly alkaline to phenolphthalein), for table I shows that still higher concentrations of these two salt solutions, containing proportionately more alkali, unquestionably accelerate diastatic activity.

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So far as the writer has been able to learn, such retardation with dilute concentrations of sodium and potassium chlorides has not been recorded heretofore. KUEBEL,[20] working with saliva, showed a slight decrease in the acceleration of hydrolysis at low concentrations of these two salts, but found no retardation such as is shown in table I, m/128 being the most dilute solution he used. This writer found a maximum acceleration between m/32 and m/128 for these two salts, and a retardation with high concentrations. He used a colorimetric method for determining the velocity of hydrolysis, comparing with tubes of colored liquids the various colors produced by the addition of iodine after a given time period. It is possible that results thus obtained may not be comparable with those of the present investigation, as the time intervals of transition between the different colored dextrins and between the last colored product formed, and achroodextrin may not be in the same proportion when the enzyme is activated by a salt as when no salt is added. Of course it must also be remembered that KUEBEL's enzymatic mixture was saliva, while that here studied was barley diastase.

GRUTZNER,[21] using the same method of estimating diastatic activity as did KUEBEL, but working with pancreatic amylase, found the optimum concentration of sodium chloride to be between m/8 and m/32.

For dialyzed ptyalin COLE found a slight decrease in the acceleration with m/3000 sodium chloride, though acceleration at this point was still considerable. He found the point of maximum acceleration to lie between m/4 and m/300. Experiments have been carried out upon the effect of sodium chloride on diastatic action by other investigators, with varying results.

Calcium and magnesium chlorides, used singly, affect hydrolysis somewhat differently from the two monovalent salts. A decided retardation is evident at high concentrations, molecular for the calcium salt and m/2 for that of magnesium. This is in marked

[20] KUEBEL, F., Über die Einwirkung verschiedener chemischer Stoffe auf die Thätigkeit des Mundspeichels. Archiv für die gesammte Physiologie 76:276–305. 1899.

[21] GRUTZNER, P., Über die Einwirkung verschiedener chemischer Stoffe auf die Thätigkeit des diastatischen Pankreasfermentes. Archiv für die gesammte Physiologie 91:195–207. 1902.

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contrast with the strong acceleration evident for sodium and potassium chlorides even at much higher concentrations. The points of maximum acceleration for calcium and magnesium chlorides, as here determined, occur at a concentration of m/64 for the former and of m/8 for the latter. From these points the acceleration falls with the gradual decrease in salt content to m/4096 calcium chloride, which accelerates but slightly, and to m/8192 magnesium chloride, which is apparently without influence. No retardation at low concentrations, as in the case of the monovalent salts, is here apparent.

The effect of the salts of the heavy metals on diastatic action (with the possible exception of mercury) have not received as much attention as those of the alkalies or the alkaline earths, which are so uniformly present in the environment of most organisms. From table VII it is apparent that the chlorides of iron and copper, as used in this investigation, retard diastatic action markedly even when present in very small quantities. Acceleration occurs in very dilute solutions, as compared with the accelerating concentrations of the other salts, the region of acceleration being found to lie between concentrations of m/2048 and m/8192 for cupric chloride, and between those of m/2048 and m/32,768 for ferric chloride, with maximum accelerations at m/2048 and m/8192, respectively. WOHLGEMUTH,[22] working with salivary diastase, found that colloidal solutions of these metals in comparatively dilute concentrations retarded diastatic action. He did not find the strong acceleration which is so apparent in the present investigation, possibly because of the fact that his metals were in colloidal condition, or because of the few concentrations that he employed. According to the data here presented, calcium chloride appears to be exceptionally effective in accelerating diastatic action, which is in accord with the findings of LISBONNE,[23] working upon the effect of this salt in restoring the activity of dialyzed salivary and pancreatic amylases in the presence of demineralized starch.

[22] WOHLGEMUTH, J., Untersuchungen über Diastasen. Biochem. Zeitschr. 9:10–42. 1908.

[23] LISBONNE, MARCEL, Influence des chlorures et de phosphates sur la saccharification de l'amidon déminéralisé par les amylases salivaire et pancréatique. Compt. Rend. Soc. Biol. 70:207–209. 1911.

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In the present study with ferric chloride, at a concentration of m/4096 an acceleration was found slightly higher than any obtained with the various concentrations of copper and of calcium. It is interesting to note here the high concentrations of copper that are favorable to diastatic action, in comparison with the great toxicity of this salt toward plants as observed by KAHLENBERG and TRUE,[24] STEVENS,[25] DUGGAR,[26] LIVINGSTON,[27] and others.

A comparison of the different degrees of the acceleration of diastatic action resulting from the presence of the various salts used singly brings out the point that the effects of potassium chloride and of sodium chloride are much the same; which is in agreement with the work of KUEBEL, GRUTZNER, COLE, WOHLGEMUTH, and others, for extract of pancreas and salivary diastase. Calcium chloride, as shown in the tables, accelerates more than do the salts just mentioned and also more than does magnesium chloride. This is not in accord with the results of WOHLGEMUTH, who, however, used only a single concentration of calcium and magnesium chlorides, this being the optimum concentration for sodium chloride as he found it, a consideration which probably accounts for the discrepancy here mentioned.

EFFECT OF SALT COMBINATIONS

The average ratios of diastatic efficiency furnish a means for attacking the problem which led to the present studies, whether or not two salts simultaneously present in a mixture influence each other's effects on starch hydrolysis. While the data obtained in these experiments are not sufficiently complete to warrant quantitative consideration of this problem, several points are at least qualitatively indicated. It is apparent that, since different concentrations of the same salt produce markedly different effects

[24] KAHLENBERG, LOUIS, and TRUE, RODNEY H., On the toxic action of dissolved salts and their electrolytic dissociation. BOT. GAZ. **22**:81–124. 1896.

[25] STEVENS, F. L., The effect of aqueous solutions upon the germination of fungus spores. BOT. GAZ. **26**:377–406. 1898.

[26] DUGGAR, B. M., Physiological studies with reference to the germination of certain fungus spores. BOT. GAZ. **31**:38–66. 1901.

[27] LIVINGSTON, BURTON EDWARD, Chemical stimulation of a green alga. Bull. Torr. Bot. Club **32**:1–34. 1905.

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upon the process of starch hydrolysis, any single treatment may be regarded as a combination of two separate applications of the salt in question, each at a lower concentration. The data above presented show that increasing the concentration of any salt almost never results in a proportionately increased effect upon hydrolysis. Sometimes such an increase completely reverses the direction of the effect, as when an increase in the concentration of sodium chloride from m/128 to m/32 produces an alteration in the efficiency ratio from 0.85 to 1.42. Another example of this is furnished by calcium chloride, for which a change in concentration from m/4 to molecular is accompanied by an alteration of the salt effect on diastatic action, from 33 per cent acceleration to a quantitatively undetermined, but nevertheless exceedingly marked, retardation. In most cases increased concentration of a single salt does not change the direction of the effect, but simply alters its intensity, as when an increase in the concentration of sodium chloride, from m/8 to m/2, results in decreasing the acceleration of hydrolysis from 82 to 71 per cent. It is to be expected, therefore, that the bringing of two different salt treatments into combination may frequently result in the same sort of effect as that produced by increasing the concentration of one of the single salts, the total salt concentration remaining the same as before. This is the true condition of affairs in many instances, and the specific question which confronts us—without attempting any precise quantitative comparisons—is whether combinations of two salts produce more or less effect upon starch hydrolysis than would either salt alone, at the higher concentration that obtains in the combination. Put in another way, the problem is this: if a portion of the amount of a given salt in a diastase mixture be replaced with a molecularly equal amount of another salt, is the resulting alteration in the effect upon hydrolysis merely that traceable to dilution of the first salt together with that due to addition of the second (as would be expected if the combined treatments were without effect upon each other), or is this alteration of a different character? Despite the incompleteness of the data at hand, study of the tables brings out several points bearing upon this question, which are made still more clear if graphs are resorted to. The more striking of these points will now be mentioned.

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In the case of the two monovalent salts, with concentrations in the region of m/16 (where the accelerating influence of the single salts is marked, without attaining its maximum), the acceleration of diastatic action produced by combination (molecular proportions 1:1) is notably greater than that produced by either single salt. At the highest concentration used (m), however, the reverse of this proposition holds, and the combination is not as favorable to diastatic action as are the single treatments.

The four series of combinations involving sodium chloride or potassium chloride with the chloride of calcium or magnesium generally show efficiencies which follow somewhat closely those for the bivalent salt of the combination. With combinations of sodium and calcium chlorides (molecular proportions 2:1; equivalent proportions 1:1), in lower concentrations (where the calcium salt alone accelerates more markedly than does that of sodium) the efficiencies, higher than for the sodium salt alone, are not as high for the combination as for calcium chloride alone. In concentrations from 3m/64 to 3m/16 the combination results in greater acceleration than does either single treatment.

Combinations of sodium chloride and magnesium chloride (molecular proportions 4:1, equivalent proportions 2:1) show no cases where the tendency to accelerate hydrolysis is pronouncedly greater than that resulting from one of the single salts. It is best here, for the most rapid hydrolysis, to use magnesium chloride in lower concentrations (where it alone accelerates more) and to use sodium chloride in higher concentrations (where this salt accelerates more).

In concentrations of the region of m/32 the efficiencies for calcium chloride alone are markedly greater than for the combination of this salt with potassium chloride (molecular proportions 2:1; equivalent proportions 1:1), although the partial concentrations of the latter salt, when singly applied, possess a decided accelerating effect. At the concentration 3m/16, diastase efficiency for the combination used is greater than for either salt alone at concentrations nearest 3m/16.

The relations which hold for combinations of potassium chloride and magnesium chloride (molecular proportions 4:1; equivalent

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proportions 2:1) are similar to those which obtain for combinations of sodium chloride with the magnesium salt. It appears that the combination is here never more favorable for starch hydrolysis than the single salt treatments.

In combinations of magnesium chloride with calcium chloride (molecular proportions 2:1) the efficiencies appear to follow those of the calcium salt, the magnesium in this combination seeming to have acquired as great efficiency for the acceleration of hydrolysis as that which characterizes the portion of the other salt which it replaces.

With combinations of copper chloride and ferric chloride (molecular proportions 1:1) the efficiencies generally lie between those for the single-salt treatments of the same concentration, as though the effectiveness of the combination were the mean influence of the two component partial treatments. No increased efficiency is here brought out by replacing a portion of one of these salts with a molecularly equal portion of the other.

While the considerations just presented appear to lead to the conclusion that certain concentrations of salt combinations may favor greater diastatic activity than do the same concentrations of either salt alone, yet it is obvious that sufficient information is not yet at hand to allow any attempt at generalization. The suggestion becomes patent that the study of properly balanced salt combinations, in their relation to enzymatic action, may add much not only to our knowledge of this persistently vague province of physiology, but also to our ability to control these important processes.

THEORETICAL CONSIDERATION OF RESULTS

In connection with the general problem of the nature of the acceleration and retardation of diastatic action by electrolytes, the results of the investigations of COLE deserve careful consideration. In a research carried on with dialyzed ptyalin, this author formulated a hypothesis to account for the influence of electrolytes on enzyme action, which to quote him directly is as follows (*op. cit.* p. 211): "The hydrolysis of starch by ptyalin is accelerated by the presence in the solution of electronegative ions (anions) other than hydroxyl ions and depressed by the presence of electro-

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positive ions (kations) and by hydroxyl ions." He considers the effect of electrolytes on the rate of action to be compounded of two factors: (1) "the acceleration due to the anion; (2) the depression due to the kation." The work of this author showed that the addition of a small quantity of hydrochloric acid to a chloride in optimum concentration for diastatic hydrolysis did not result in an added acceleration, but in a decreased activity. This he accounted for by considering the acceleration produced by the chloride as due to the chlorine ions, these being already in optimum concentration before the addition of the acid; hence when more chlorine ions were added with the acid there could be no further increase in diastatic activity. The observed decrease in enzyme efficiency, which accompanied the putting in of the acid, was explained as due to the increased concentration of retarding cations which must result from the presence of the acid and to the destruction of ferment by the hydrogen ions. The salt present in a molecular condition is not taken into consideration.

This hypothesis appears to explain many of the phenomena of salt influence upon diastatic action as found in these studies. It does not, however, offer an explanation for the retardation of diastatic action by low concentrations of sodium and potassium chlorides. COLE suggests also that all cations seem to retard diastatic action alike, which would seem questionable from the standpoint of the results obtained in the present investigation.

WOHLGEMUTH, investigating the effects of certain salts on the hydrolysis of starch by pancreatic amylase, using a colorimetric method for determining the rate of hydrolysis, concludes that the acceleration caused by a chloride is due to the chlorine ion. BANG,[28] working with dialyzed ptyalin and determining the amount of a reducing dextrin formed from soluble starch in a given time, as a measure of the rate of hydrolysis, agrees with WOHLGEMUTH in this.

MCGUIGAN, working with malt diastase and using as a criterion for comparing the different salt effects the inhibition of the formation of any reducing sugar in a certain time period, takes a view opposite to that of COLE. He considers the acceleration of enzyme

[28] BANG, IVAR, Untersuchungen über Diastasen. Biochem. Zeitschr. 32:417–442. 1911.

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action brought about by a salt as due to the effect of the cation and the retardation as due to the anion. Although his results are not directly comparable to those of the present investigation, it may be noted that most of the salt effects here brought out may be explained by this theory about as satisfactorily as by that of COLE. It is manifestly impossible, however, from the evidence brought out in this investigation, to decide whether either theory is adequate to explain satisfactorily the phenomena of acceleration and retardation of diastatic action by electrolytes. It is, of course, probable that diastatic action is, in some measure, affected by the presence of salts in a molecular condition, also that certain salts form compounds with the enzyme itself, or with other organic bodies which are present in the diastatic mixtures that have usually been used in experimentation of this sort. Likewise diastases of different origins may be influenced quite differently by the same electrolytes. Further and more careful experimentation, with refinement of methods as suggested by FORD,[29] SHERMAN, KENDALL and CLARK, FRANKEL and HAMBURG,[30] and others, are still much needed.

Summary

The present investigation deals with the effects of sodium, potassium, calcium, magnesium, cupric, and ferric chlorides, alone and in certain binary combinations, on the hydrolytic activity of Merck's "diastase of malt absolute," the enzymatic mixture acting on a boiled solution of washed maize starch, at 50° C. The disappearance of the ability of the starch to give a color reaction with iodine was taken as the end point of the reaction, and the reciprocal of the time period which elapsed before this end point was attained (considering the time period of the control without added salt as unity) was used as a measure of the intensity of enzyme action.

A wide variation is clearly shown in the influence of the different chlorides upon diastatic action, which is probably to be related to the properties of the various cations employed. More or less

[29] FORD, JOHN S., Lintner's soluble starch and the estimation of diastatic power. Jour. Soc. Chem. Ind. 23:414–422. 1904.

[30] FRANKEL and HAMBURG, Über Diastase. Beitr. Chem. Physiol. u. Path. 8:389–398. 1906.

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pronounced acceleration of starch hydrolysis is shown for all of the salts used at different concentrations; the highest acceleration found is for iron (291 per cent) and the next highest for calcium (269 per cent). Retardation of hydrolysis is shown at high concentrations for all salts excepting sodium chloride and potassium chloride. For these two salts a pronounced retarding action (15 per cent in both cases) is manifest at low concentrations, the greatest retardation occurring with concentration m/128. This retardation in weak solution seems not to have been considered heretofore.

Combinations of two salts are shown to be sometimes more and sometimes less efficient in modifying diastatic action than are molecularly equal concentrations of their component salts. It is thus possible that enzymatic power, the magnitude of which is frequently to be related to the concentration of single salts in the medium, may in some cases at least be still more highly developed than is possible through the influence of single salts, by the presence of a properly balanced salt combination.

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A PHYSIOLOGICAL AND CHEMICAL STUDY OF AFTER-RIPENING

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 170

SOPHIA ECKERSON

Many seeds and spores require a long time for germination. The term "after-ripening" has come into rather general use to designate the changes in the seed during this period. It is often loosely used to include disintegration of the seed coats as well as protoplasmic or metabolic changes in the embryo. It seems better to limit its use, as has been done in this laboratory, to those cases where the delay is due to characters of the embryo. In the majority of seeds thus far investigated, the delayed germination is due to the exclusion of water or of oxygen by the seed coats. A few seeds have been studied, however, which do not grow when all coats have been removed and the embryo put in good germinating conditions. Some change within the embryo is necessary before germination, that is, lengthening of the hypocotyl, can take place. This process is what we mean by "after-ripening."

NOBBE and HANLEIN (45), WIESNER (52), JOST (29), and others assume, in cases where water enters the seed coat, that growth after a long period is due to some change going on within the embryo during the seemingly dormant period. This has been determined definitely for only three or four species.

LAKON (35) finds that the delayed (1–2 years) germination of *Pinus silvestris*, *P. Strobus*, and *P. Cembra* is not due to coat characters. With the coats broken or removed, the time required for germination was not shortened. Seeds of *Fraxinus excelsior* (36) sown in the spring do not germinate until the following spring. In the mature seed the embryo occupies about half the space within the endosperm; the rest is occupied by a mucilaginous substance. During the year that the seed lies in the ground, the embryo grows in length and fills the seed coat. Since the embryo is fully mature at maturity of the seed, but a period of growth is

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necessary before germination, LAKON calls this "Vorkeimung" instead of "Nachreife."

Many methods have been used by different workers in the attempt to shorten the resting period of buds and bulbs. The first of these is JOHANNSEN'S (30) treatment with ether. He found that growth could be hastened at the beginning of and near the end of the resting period, but not in the middle period. MOLISCH (40) immersed shoots in water at 35° C., and the buds opened earlier than those on untreated shoots. IRAKLIONOW (23) finds that the warm bath increases respiration only in the first days, then the respiration curve falls to its original height. MÜLLER-THURGAU and SCHNEIDER-ORELLI (42, 43) used the warm bath method to hasten the germination of potato tubers, and lily of the valley bulbs. They find the sugar content increased by the warm bath, but this is immediately used by the increased respiration. Unless the bulbs are kept at a high temperature, there is no lasting effect. Zero temperature increases the sugar content and the respiration; injury produces a slight increase in sugar content. They do not believe that hastened growth in these cases is due to increased sugar content, but rather that the high temperature has some effect on the protoplasm. CHRISTENSEN (3) made chemical analyses of resting and growing bulbs, but found no appreciable differences. He concluded that the slow growth of resting bulbs was not due to lack of soluble food materials.

WEBER (53) and JESENKO (27) found that injury to the buds hastens their development. Later, JESENKO (28) found that the shoots from these buds were abnormal. Shoots immersed in dilute solutions of alcohol, H_2SO_4, and other substances, develop normally and more rapidly than untreated shoots. LAKON (37) forced the development of winter buds by standing the cut ends of shoots in Knop's solution. MOLISCH (41) has recently found radium emanations effective.

All these various methods shorten somewhat the rest period of bulbs and winter buds. Little has been done to determine what is the limiting factor to growth in these cases and what internal change is produced by the external application.

CROCKER (4, 5) found that the long period required for germina-

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tion of seeds of hawthorn is due in part to seed coat characters and in part to characters of the embryo. With testas removed, in light at room temperature, the cotyledons increase greatly in size and turn green, but only a small percentage (2–5 per cent) of the hypocotyls grow.

DAVIS and ROSE (**6**), working in this laboratory, studied further the germination of seeds of *Crataegus mollis*. They find that under ordinary conditions seeds with carpels intact require one year or more for germination. Embryos with carpels removed, but with testas intact, germinated after 90–96 days at 5–6° C.; 74 per cent germinated after 75 days in the cold when removed to the warm greenhouse. With both carpels and testas removed, after 28 days at 6° C. 78 per cent germinated in 5 days in the greenhouse. Thus with all coats removed there is still a delayed germination due to characters of the embryo itself, a period of "after-ripening" necessary before elongation of the hypocotyl can take place. It has been my purpose to study the changes within the embryo during this period.

Investigation

I have made a preliminary microchemical study of the chemical changes during after-ripening. These results form the basis for a quantitative study. This paper gives the results of the microchemical study, together with quantitative determinations of the substances in the embryo at different periods during after-ripening.

DAVIS and ROSE (**6**) found the best conditions for after-ripening to be a temperature of 5–6° C. This inhibits growth of the cotyledons and is favorable for the metabolic changes within the hypocotyl. I studied the after-ripening of several species of *Crataegus*.

Seeds with testas intact were soaked 16 hours at 5° C., were washed thoroughly by shaking in a bottle of distilled water (to prevent mold), and put in dishes on moist cotton in the ice chest at 5–6° C. Microchemical tests were made once a week during the after-ripening period. Sections were preserved in glycerin for comparison.

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MICROCHEMICAL METHOD

In order to detect the metabolic substances of the cell as nearly unchanged as possible, observations must be made on the living tissue. Sections were made on a freezing microtome or free-hand, and *intra-vitam* stains (8) were used. Of the different methods and stains used, the following were found to be the most valuable.

Fats.—Soudan III or Scharlach R, dissolved in 50 per cent alcohol. All fats are soluble in these stains.

Lecithin.—The fats were first dissolved out with acetone, in which lecithin is not soluble. It was then stained with Soudan III, or blackened with fumes of osmic acid.

Starch.—The sections were first heated in water on the slide, and then a drop of iodine solution added.

Sugar.—For the reducing sugars Fehling's solution was used as follows. The sections were heated in the copper sulphate solution, on the slide. The other part of Fehling's solution, Rochelle salt and sodium hydroxide, was then added. Copper oxide is deposited in the cells containing sugar. Still better is the osazone test as modified by MANGHAM (38). Dissolve phenylhydrazine hydrochloride and sodium acetate in 10 times their weight of glycerin; warm to dissolve; filter once or twice. To use, put a drop of each on the slide, mix, put section of tissue in same. Place slide in warm oven 5–30 minutes, and then cool. Osazone crystals will be formed in the cells which contained sugar.

Acidity or alkalinity.—Neutral red, sulphate of Nile blue, Dahlia violet, and methyl orange. A 1/5000 solution of neutral red is sensitive to N/11,000 NaOH; a 1/5000 solution of sulphate of Nile blue is sensitive to N/5100 NaOH; the others are less sensitive (9).

Catalase.—A drop of H_2O_2 was put on the section on the slide and evolution of oxygen noted.

Oxidase.—A few drops of freshly made solution of guaiaconic acid, on the slide.

Peroxidase.—A drop of H_2O_2 added to a few drops of guaiaconic acid, put on the sections on the slide.

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TABLE I

CONDITION OF THE EMBRYO OF CRATAEGUS GLORIOSA

Glucoside amygdalin	Condition of seeds	Fatty oil	Lecithin	Protein	Sugar	Starch	Catalase	Peroxidase	Oxidase	Acidity
	Air-dry	Abundant (25 to 30 per cent)	x	x	o	o	x	Hyp. little Cot. x	o	Hyp. basic Cot. acid
HCN.....	After-ripened	Slight decrease	x	x	Trace	o	Slight increase	Great increase	x	Great increase
	At germination	Decrease	x	x	x	x	x	x	x	x

The value of neutral red as an indicator has been questioned by many. If the change in color of a dye is due to H ion content, it can safely be used as an indicator. FRIEDENTHAL (13) gives a very valuable series of indicators with the H or OH ion concentration which will produce a change in color. In the presence of substances which form combinations with the dye, the change in color would be no indication of H or OH ions. In all my work, however, the acidity or alkalinity as shown by neutral red was confirmed by titrations with NaOH or HCl.

Microchemical tests should be followed always by quantitative determinations at the critical points. When so used the method is reliable and is a great saving of time and material.

RESULT OF MICHROCHEMICAL TESTS

The condition of the embryo at the beginning and end of the after-ripening period, and at germination just after the hypocotyl has pushed out through the testa, is shown in the accompanying table (I). In all the tables, x indicates presence in quantity, and o indicates absence.

There is a very gradual, though constant, increase in the acidity and in the enzymes during the whole period. After 80–90 days at 5° C.,

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when the acidity has almost reached its maximum, the fats begin to break up and sugar appears. Oxidase first appears at this time. Hydrocyanic acid appears after 75 days, increases up to germination, then decreases (19, 49).

WATER-HOLDING POWER

Since the hypocotyls of the air-dry seeds are basic, while the cotyledons are acid, it was thought that they might have less ability to take up water than the cotyledons. To test this, seeds were taken at different stages of after-ripening, the coats removed, and the naked embryos soaked in water for 5 hours. These were then dried carefully with filter paper and, after the hypocotyls were separated from the cotyledons, were put in separate weighing bottles. These were weighed, then heated in an oven 10 minutes at 100° C., removed from the oven, and dried at 50° C. Many determinations were made. The accompanying table (II) gives a typical series.

TABLE II

WATER-HOLDING POWER OF EMBRYO OF CRATAEGUS GLORIOSA

	Hypocotyls			Cotyledons		
	Wet weight grams	Dry weight grams	Percentage water	Wet weight grams	Dry weight grams	Percentage water
Coats removed and soaked 5 hrs.	0.0157	0.0121	23	0.2690	0.1542	42
90 days at 5° C.	0.0189	0.0116	38	0.2700	0.1744	35
Germinated (hyp. 3 mm.)	0.0289	0.0115	60	0.2094	0.1260	39

ACIDITY

Determinations of acidity were made at the same periods of after-ripening as the water determinations (table III). The embryos were washed in distilled water which had been boiled to expel CO_2.

It will be seen that the metabolism of the fats does not begin until the acidity has reached a certain amount, the water content has increased greatly, and the enzymes are set free. The hypocotyl does not elongate until that time. It has long been known that

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considerable free fatty acid is formed during the germination of oily seeds (GREEN **17**, SCHMIDT **50**). MILLER (**39**) finds, in the germination of *Helianthus annuus*, that the quantity of free acid in the hypocotyl increases rapidly at the beginning of germination.

IVANOW (**24, 25, 26**) studied the metabolism of fats in ripening and in germinating seeds. He finds that the rapidity of oil transformation in germinating seeds depends on the fatty acid components of that particular oil. The oil of flax and of hemp contains

TABLE III

ACIDITY OF EMBRYO OF CRATAEGUS GLORIOSA

	Hypocotyls			Cotyledons			
	Grams	N/20 KOH cc.	N/20 KOH cc. per gram		Grams	N/20 KOH cc.	N/20 KOH cc. per gram
Air-dry	0.0267	Slightly basic	0.00	Air-dry	0.5374	0.20	0.37
30 days	.....	.....	0.10	30 days	.....	....	0.40
60 days	.....	.....	0.30	.....	.....	....	....
90 days at 5° C. (hyp. 2 mm.)	0.0444	0.04	0.90	Cots. white	0.8162	0.35	0.42
Germinated (hyp. 2.5 cm.)	0.360	0.45	1.24	Cots. yellow	0.1914	0.60	3.13
Germinated (hyp. 3.5–5 cm.)	0.5967	0.65	1.09	Cots. green (in light 1 week)	0.3907	1.20	3.07
Germinated (hyp. 3–5 cm.)	0.3810	0.60	1.57	.....	0.7099	1.90	2.67

the less saturated acids—linolenic and linoleic—and is transformed much more quickly than that of rape, which contains oleic acid. The less saturated acids disappear rapidly (forming carbohydrates) from the seedlings and cause the very low acid number of flax and hemp. Unsaturated acids of the oleic acid type are more stable and inactive; therefore rape shows a higher acid number than flax or hemp. The acids in the seeds of *Crataegus* were not identified; this will be done later.

DELEANO (**7**) studied the chemical changes during the germination of *Ricinus communis*. He finds that the acidity and the

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catalase increase up to a maximum, which is reached on the eighth day of germination (the hypocotyl is then 2.5 cm. long). Then the fats begin to break up and within two or three days disappear. The fats are transformed into a soluble substance of the character of a plant mucilage. This is later transformed into sugar, cellulose, and other substances. DELEANO says that the acids activating hydrolysis are formed during germination; he detected acetic and lactic acids. He thinks that catalase is directly concerned with hydrolysis of the fats. This is doubtful, however, since catalase is so universally present. Peroxidase reached a maximum about the fourteenth day of germination (the hypocotyls were 8.5 cm.).

The chemical changes during the 90 days of after-ripening of *Crataegus* are the same as those of the first 8 days of germination of *Ricinus*. It is as though the chemical processes, telescoped in *Ricinus*, are drawn out in *Crataegus*.

Seeds of the crab apple (*Pyrus baccata*) after-ripen in 30 days at 5° C. At the beginning of their after-ripening period, hypocotyls of these embryos have an acidity and a water-holding power slightly greater than those of *Crataegus* after 60 days at 5° C. (hypocotyl 1.45 cc., N/20 KOH, moisture 48 per cent; cotyledons 0.368 cc., moisture 39 per cent). Peroxidase increases gradually from a very little in the air-dry seeds to a considerable amount at germination. As in *Crataegus*, oxidase does not appear in hypocotyls of *Pyrus baccata* until immediately before germination.

EFFECT OF ACIDS

FISCHER (11) finds that when seeds of water plants (*Alisma*, *Sagittaria*, and *Sparganium*) are treated with dilute solutions of acids, or the strong alkalies KOH and NaOH, the percentage of germination is increased. He conceives the H ions of the acids, and the OH ions of the alkalies as destroying the equilibrium of the cell and starting up the chemical processes.[1] Seeds treated with solutions of the fatty acids (formic, acetic, propionic, and butyric) did not germinate. He therefore considers these acids toxic; but he used too concentrated solutions. In dilute solutions the

[1] CROCKER has found that these seeds germinate readily if the coats are broken or removed. The protoplasm is not dormant.

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fatty acids shorten the after-ripening period of both hawthorn and apple.

Mlle. PROMSY also used acetic acid with good results on seedlings of tomato and corn. She studied (47, 48) the effect of acids on the respiration of germinating seeds of tomato, corn, barley, *Dioscorea*, and *Elaeis guineensis*. She finds that organic acids (citric, malic, oxalic, tartaric, and acetic) increase the respiratory quotient and at the same time the intensity of respiration, measured by evolution of CO_2. Inorganic acids, on the other hand, do not modify the quotient, except in the single case of the fatty seeds of *Elaeis*. Seeds were soaked in a solution of the acid for 24–48 hours, then put in germinative conditions in sand, and the sand watered with the solution. Seedlings submitted to the action of organic acids grew more rapidly than the control, increased more in wet weight, and increased more in dry weight, if determined at the end of the germination period when the plants were green. Seeds treated with inorganic acids, HCl and H_2SO_4, germinate more quickly than the control. The wet weight of seedlings is increased, dry weight is the same as the control.

MARTIN FISCHER (12) found that acids greatly increase the absorption of water by colloids, while salts decrease the absorption. He studied the absorption of water by gelatin, fibrin, and frog muscle.

A certain degree of acidity seems to be necessary before germination of *Crataegus* seeds. The acidity of the hypocotyl develops very slowly and little water is absorbed in the early stages of after-ripening. It was thought that absence of free acids might be the limiting factor to growth. An attempt was made to supply this by soaking the seeds in acid before putting them in after-ripening conditions.

METHOD OF TREATMENT WITH ACIDS

Seeds of *Crataegus*, with carpels removed but testas intact, were soaked in the acid solution over night at 5° C., washed, and put on moist cotton in Petri dishes. At the end of 14 days they were washed carefully, the coats removed, and the embryos washed in distilled water. They were then tested for presence of free enzymes. In the accompanying table (IV) the results are given

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in order of the depth of color of the reaction for peroxidase and oxidase.

TABLE IV

ENZYMES IN HYPOCOTYLS OF CRATAEGUS DUROBRIVENSIS

	Catalase	Peroxidase	Oxidase
Air-dry at 5° C. 14 days	Very little	Very pale	0
Control	Little	Light blue	0
N/1000 HCl	x	Light blue	0
N/100 acetic	x	Slightly darker	0
N/50 butyric	x	Slightly darker	?
N/70 butyric	x	Darker	Trace
N/3400 HCl	x	Darker	Trace
N/1000 acetic	x	Like after-ripened	Dark blue
After-ripened 90 days at 5° C	x	Dark blue	Dark blue
Germinated	x	Deep blue	Darker

In 14 days embryos treated with N/1000 acetic acid attain an enzyme reaction equal to that of the untreated embryo after 90 days' after-ripening. Both N/3400 HCl and N/70 butyric show a great increase in enzymes over the control.

The acidity was determined in several cases. The testas and embryos were always carefully washed in boiled distilled water to prevent any trace of external acid vitiating the results. The accompanying table (V) gives the results of one series.

TABLE V

ACIDITY IN EMBRYOS OF CRATAEGUS DUROBRIVENSIS

In acid over night	Hypocotyls			Cotyledons		
	Grams	N/20 KOH cc.	N/20 KOH cc. per gram	Grams	N/20 KOH cc.	N/20 KOH cc. per gram
Control	.....	Slightly basic	....	.....	....	0.37
N/70 butyric 16 hours	0.0184	Neutral	0.00	0.3544	0.16	0.45
N/70 butyric 14 days at 5° C	0.009	0.01	1.11	0.3138	0.65	2.06
N/100 acetic 14 days at 5° C	0.0119	0.02	1.68	0.2420	0.40	1.65

After seeds have been in N/70 butyric acid 16 hours, the outer cells of the cortex of the hypocotyl give an acid reaction with Dahlia

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violet. The inner cells are still basic. This shows that the acid had penetrated a little way. The inner cells develop acidity much more rapidly than in the control.

Of seeds treated as above with N/70 butyric acid, and after-ripened at 5° C. with testas on, 52 per cent germinated in 53 days; the others decayed. The testas were removed from a lot of seeds after soaking in N/70 butyric acid, and the naked embryos kept on moist cotton at 5° C.; these germinated in 16 days. As shown by the large number of seeds which were killed, N/70 butyric is too strong. More dilute solutions are being used now.

N/800 butyric has about the conductivity of N/1000 acetic and N/3400 HCl, which were found to be effective; therefore that is being tested as well as still more dilute solutions. The more dilute solutions are not toxic, instead they greatly increase the rate of the process of after-ripening; therefore, germination is hastened. The after-ripening period of seeds with testas intact was shortened from 80–90 days to 45–53 days; with testas removed, from 30 days to 16–18 days.

Summary

Condition of the embryo in dry storage.—Food is stored in the embryo in the form of fatty oil; there is also considerable lecithin; neither starch nor sugar is present. The reaction of the cotyledons is acid, but the hypocotyl is slightly basic. The water-absorbing power of the hypocotyl is less than 25 per cent of the wet weight.

There is a series of metabolic changes in the embryo during the period of after-ripening. The initial change seems to be an increased acidity. Correlated with this is an increased water-holding power, and an increase in the activity of catalase and peroxidase.

Near the end of the period of after-ripening there is a sudden increase in the acidity, and in the water content; here oxidase first appears. All of these increase until the hypocotyl is 3–5 cm. long. At this time the fats decrease and sugar appears. Hydrocyanic acid is present in the cotyledons.

The after-ripening period can be greatly shortened by treating the embryos with dilute acids, HCl, butyric, and acetic. The water-holding power, the acidity, and the amount of peroxidase increase much more rapidly, and oxidase appears much earlier, than in untreated embryos.

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It is evident that there is a correlation between acidity of the hypocotyl of *Crataegus*, its water-absorbing power, production of enzymes, and germinating power. Whether the acidity is causal or merely correlative is not known. There is some evidence, however, that it is causal. GREEN (**17, 18**) has shown that it leads to the liberation of enzymes; and MARTIN FISCHER (**12**) that it increases the water-absorbing power of colloids. Other dormant seeds of the Rosaceae are now being studied with the hope of gaining further knowledge on this point.

Acknowledgments are due Dr. WILLIAM CROCKER, under whose direction the work was done.

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THE CALIFORNIA PAROSELAS

S. B. PARISH

(WITH FIVE FIGURES)

This paper is based on a study of the ample collections in the herbarium of the University of California, and of the material in the private herbaria of Dr. A. DAVIDSON and of the writer. While the numerous extralimital material in these collections has been carefully studied, the citation of specimens is confined, for the most part, to those collected within the boundaries of the state. Dr. HALL not only placed the collections of the University at the writer's disposal, but allowed him the use of a preliminary study which he had prepared, and most generously aided him in other ways. For the drawings, from which the figures have been reproduced, the writer is under obligations to the skillful pen of Mrs. CHARLOTTE M. WILDER.

The generic name

The genus *Dalea* was founded by LINNAEUS in 1737, in his *Hortus Cliffortianus*, but in the *Species Plantarum* of 1753 he reduced it to *Psoralea*. The latter year being now accepted as the initial date for phanerogamic nomenclature, we are debarred from going back to LINNAEUS' earlier use of the name. It was revived by JUSSIEU in 1789, and according to present rules that must be taken as the authoritative date for the name, and it is with this citation that it is maintained in the new GRAY'S *Manual*.[1] Unfortunately, in the interval it had been used for two other genera. In 1756 P. BROWN applied it to what is now universally regarded as *Eupatorium*, so that, as a synonym, his use may be disregarded. But GAERTNER, in 1788, gave it to what ENGLER and PRANTL and the *Kew Index* now call *Microdon* Choisy (1823). This scrophulariaceous genus, therefore, has the prior title by a single year, and the leguminous genus must take the later name *Parosela* Cav. (1802).

[1] In the *Natürlichen Pflanzenfamilien*, *Dalea* Linn. is retained.

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This needless and confusing change should have been provided against in the list of *nomina conservanda*, and it is to be hoped that the oversight may be remedied in a future revision.

Distribution

Mexico is the center of distribution of the genus, fully 120 species (119, CONZATTI) having been described from the temperate regions of that republic. Thence it extends along the Andes to Chile, where it has its southernmost representative in *Dalea multifoliata*, at 30° south latitude. Crossing the United States' boundary, it is well developed in the Lower Sonoran life-area; 17 species are found in Texas (COULTER), 19 in New Mexico (HAMMOND), and 33 in Arizona (THORNBER). The most northern species is *Parosela alopecuroides*, which reaches southeastern North Dakota, at latitude 30° N., and the same species extends east to Tennessee (GATTINGER). Besides the continental species, two outlying ones are found on the Galapagos Islands. In California it is a characteristic genus of the deserts, a single species passing into an arid border of the cismontane region.

Parosela

PAROSELA Cav. Descr. 185. 1802.—*Dalea* Juss., Gen. 355. 1789; *Asagraea* Baillon, Adansonia **9**:232. 1870.—Annual or perennial herbs, shrubs, or trees, more or less glandular-dotted. Leaves odd-pinnate, rarely simple, with minute subulate stipules. Flowers in spikes or simple racemes, rarely scattered or solitary; bracts caducous, in ours subulate and inconspicuous; calyx 5-toothed; petals all with claws, that of the usually cordate banner inserted at the bottom of the calyx, and those of the wings and keel adnate below the middle of the cleft stamineal sheath; stamens 10, rarely 9, monadelphous; anthers uniform; ovules 2, rarely 4–6; pod membranaceous or chartaceous, indehiscent, 1-seeded.

ARTIFICIAL KEY TO THE CALIFORNIAN SPECIES

Perennial herbs.

Calyx long-villous, its teeth filiform..... 1. *P. mollis.*

Calyx silky-canescent, its teeth ovate-acute.. 2. *P. Parryi.*

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Woody shrubs.
  Flowers in condensed headlike spikes.
    Stems conspicuously guttate-glandular;
      leaflets 1–5 mm. long.....3. *P. polyadenia.*
    Stems sparsely prickle-glandular; leaflets
      1–2 cm. long.....4. *P. Emoryi.*
  Flowers in loose spikes or racemes.
    Leaves pinnate, or a few simple.
      Leaves and twigs hoary-tomentose.....5. *P. neglecta.*
      Leaves and twigs appressed silky-pubescent.
        Leaflets distinct.....6. *P. Johnsonii.*
        Leaflets decurrent or confluent.....7. *P. californica.*
    Leaves mostly simple, but a few 3-pinnate..7*a*. *P. californica simplifolia.*
    Leaves all simple, glabrate .....8. *P. Schottii.*
Spinose tree, hoary-pubescent, nearly leafless...9. *P. spinosa.*

SYNOPSIS OF THE SPECIES

**Ovules 2; pod included*
†*Flowers spicate; herbs*

1. PAROSELA MOLLIS (Benth.) Heller, Cat. N. Am. Pl. ed. 2. 6. 1900.—*Dalea mollis* Benth. Pl. Hartw. 306. 1848.—Herbaceous from a perpendicular root, the spreading stems 5–15 cm. long, dotted with small, flat, brown glands, soft-villous, as are the leaves: leaflets 9–13, oblong, cuneate-oblong, obovate, or obcordate, usually retuse, 3–8 mm. long, dotted with a row of small marginal glands: flowers numerous in oblong spikes, 1–6 cm. long; calyx 6 mm. long, its teeth filiform from a triangular base, equaling or exceeding the glandular-dotted tube; corolla rose-tinted, not exceeding the calyx teeth; banner 2 mm., wings and keel 3 mm. long, the latter mostly with a small gland at base: pod obovate, hirsute, and glandless, 3 mm. long: seed brown, reniform, 2 mm. long.—Fig. 1.

Probably a short-lived perennial, sometimes flowering the first year. The flowers are on very short pedicels, bracteolate at base by a pair of swollen pointed glands, which persist on the rachis after the fall of the fruiting calyces.

TYPE.—"*In vicinibus Monterey*"; certainly an error. According to WATSON, in the *Botany of California*, it was first collected by COULTER, probably in southern Arizona.

DISTRIBUTION.—A common species in sandy and gravelly soils throughout the Lower Sonoran of the Colorado and Mojave deserts; thence northeast to southern Nevada (GOODDING 2237), southeast through Arizona (THORNBER)

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and New Mexico to Coahuila, Mexico (PURPUS 115), south to Guaymas (PALMER) and Lower California (BRANDEGEE).

SPECIMENS EXAMINED.—*Mojave Desert:* Inyo Mountains, S. W. AUSTIN 441; Panamint Cañon, May 14, 1906, HALL 6999; Bagdad, May 2, 1892, BRANDEGEE; Camp Cady, May 1882, PARISH 83; Sheephole Mountains, May 1895, HALL 6097. *Colorado Desert:* Palm Springs, April 10, 1880, PARISH 88, and April 10, 1893, DAVIDSON; Coachella, April 1905, GREATA 415, and HALL 5792; Mecca, April 1904, Mrs. M. MCKIBBEN; McCoy Wash, April 1905, HALL 5932; Borregos Spring, April 28, 1894, BRANDEGEE; Hodges Mountain, April 1905, HALL 5975; Salton, April 12, 1892, DAVY 8049; Chuckawalla Bench, December 3, 1904, E. E. SCHELLENGER 99; Palo Verde, April 1905, HALL 5956; Calexico, March 29, 1902, DAVY 8005; Dixyland, October 18, 1912, PARISH 8312.

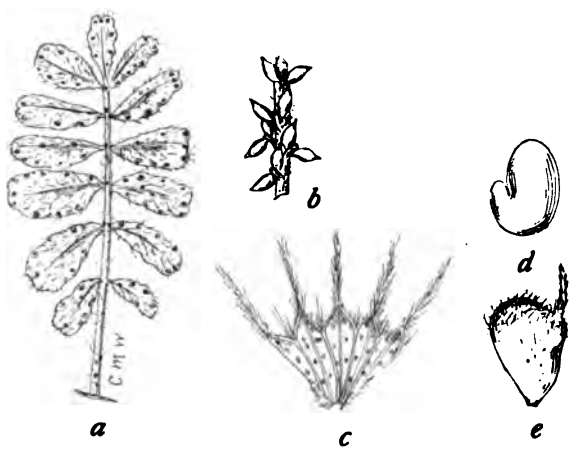

FIG. 1.—*Parosela mollis: a*, leaf; *b*, part of rachis, showing the glandular bracteoles; *c*, calyx, from the inside, to show the glands, which are concealed on the exterior by the dense hairs; *d*, seed; *e*, mature pod; *a, c, d, e*, ×3.

2. PAROSELA PARRYI (T. & G.) Heller, Cat. N. Am. Pl. ed. 2. 6. 1900.—*Dalea Parryi* T. & G., Proc. Am. Acad. **7**:397. 1868.—Perennial, the slender woody stems ascending, 1–6 dm. tall, finely and closely puberulent, or glabrate, dotted with small flat, dark glands: leaflets 3–21, oblong to obovate, obtuse or retuse, 1–3 mm. long, sparsely puberulent or glabrate, obscurely glandular-dotted or glandless: flowers numerous in pedunculate spikes 5–8 cm. long; calyx 3 mm. long, nervose, silky-canescent, obscuring the rows of small glands in the intervals, or glabrate; upper teeth triangular

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or ovate-acute, the lowest narrower and longer, about half the length of the tube; corolla minutely glandular-dotted, twice exceeding the calyx; banner broadly orbicular, 1.5–2 mm. high and as

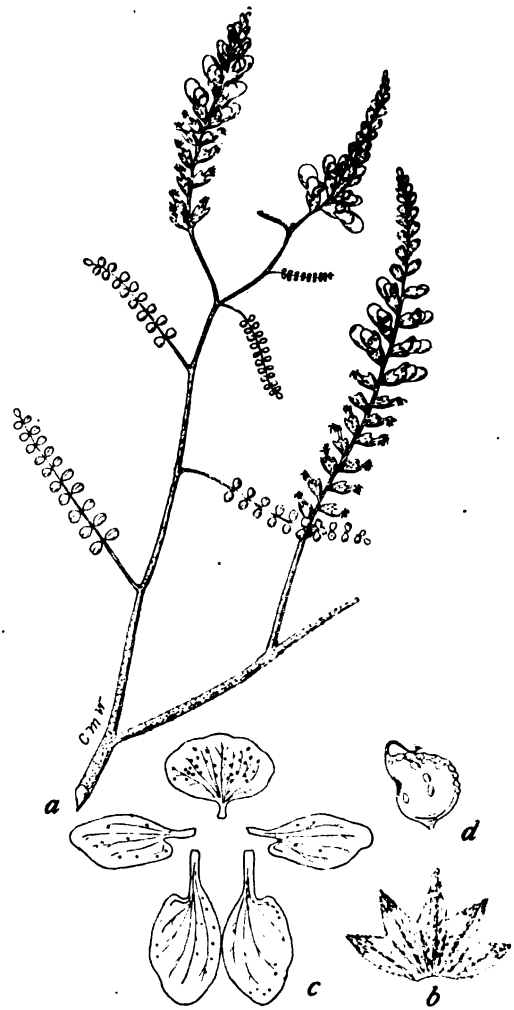

FIG. 2.—*Parosela Parryi:* *a*, branch, natural size; *b*, calyx; *c*, petals; *d*, pod; all ×2.5.

wide or wider; wings 2 mm. and keel 4 mm. long, the lower half of the banner and the upper half of the keel blue, the remainder white: pod gibbous, glandular, 2 mm. long: seed reniform.—Fig. 2.

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TYPE.—"Gravelly hills near Ft. Mohave, Dr. J. G. COOPER, and lower down on the Colorado, near the mouth of the Williams River, Dr. C. C. PARRY."

DISTRIBUTION.—Lower Sonoran of the Colorado Desert, thence to Arizona (PURPUS 8507) and adjacent Mexico (PALMER) and Lower California (BRANDEGEE).

SPECIMENS EXAMINED.—Thermal, May 1903, DAVIDSON; Mammoth Tank, March 17, 1882, PARISH 1180; Cañon Springs Wash, February 25, 1904, SCHELLENGER 63; Cane Spring, April 1905, HALL 5846; Chuckawalla Bench, December 1906, SCHELLENGER 95; Palo Verde, April 1905, HALL 5975; Virginia Dale, May 1905, HALL 6041.

Parosela Orcuttii, comb. nov.—*Dalea Orcuttii* Wats., Proc. Am. Acad. **20**:359. 1885, a species of adjacent Lower California, may be looked for near the boundary. It resembles *P. Parryi*, but the stems are not glandular-dotted, and the corolla is but little longer than the calyx teeth.

†† *Flowers in condensed spikes which are sessile at the ends of branchlets, the rachises deciduous, leaving the branchlets as a subspinose armament; calyx teeth similar, or nearly so. Shrubs, even the old wood glandular*

3. PAROSELA POLYADENIA (Torr.) Heller, Cat. N. Am. Pl. ed. 2. 6. 1900.—*Dalea polyadenia* Torr. ex Wats., Geol. Expl. 40th Par. **5**:64. *pl. 9.* 1871.—Shrub 5–10 dm. tall, sparsely spinose, the short and stout divaricate branches canescent with a dense pannose tomentum, and copiously dotted with large yellow or red guttate glands: leaves on short petioles, 1–2 cm. long; leaflets 5–11, ovate, 1–5 mm. long, tomentose and sparsely glandular; flowers numerous; spikes globose or oblong; calyx villous and glandular-dotted, 3.5–4 mm. long; teeth subulate from a broad base, nearly as long as the tube; petals rose-pink or purple, each usually with a small gland at the apex, rarely somewhat bearded, 3.5 mm. long, little exceeding the calyx teeth: pod 3–5 mm. long, pubescent above.

TYPE.—"Borders of the Truckee Desert, Nevada."

DISTRIBUTION.—Inyo County, thence into Nevada (Wadsworth, KENNEDY, Candelaria, SHOCKLEY 275).

SPECIMENS EXAMINED.—Owens Valley, PURPUS 1960.

PAROSELA POLYADENIA (Torr.) var. **subnuda,** comb. nov.—*Dalea polyadenia* Torr. var. *subnuda* Wats., Bot. Cal. **2**:441. 1880. —Glabrous or nearly so; calyx glabrous and glandular-dotted, the teeth villous-ciliate.

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TYPE.—"Owens Valley (Dr. W. MATTHEWS); Southern Utah (W. JOHNSON)."

SPECIMENS EXAMINED.—Mono County, July 1888, Mrs. J. H. HARCOURT; Owens Valley, S. W. AUSTIN 171; Owenyo, June 1911, DAVIDSON.

4. PAROSELA EMORYI (Gray) Heller, Cat. N. Am. Pl. ed. 2. 6. 1900.—*Dalea Emoryi* Gray, Mem. Am. Acad. II. **5**:315. 1855; Torr. Pac. R.R. Rep. **5**:360. *pl. 2*.—Shrub 1–2 m. high, destitute of true spines, the numerous slender intricate branches hoary pubescent and sprinkled with small brown or red prickle-shaped glands: leaves 1–9 cm. long, pubescent and sparsely glandular; leaflets 3–13, the terminal one usually narrower and longer than the lateral, rarely a few of the uppermost simple: flowers 10–20; spike globose, 1–2 cm. in diameter; calyx silky villous, 6 mm. long, colored orange by the abundant minute subulate glands; teeth linear, as long as the tube; corolla bright purple, little exceeding the calyx teeth; petals nearly equal, about 4 mm. long: pod 3 mm. long, dotted with red glands.

TYPE.—"On the desert tablelands of the Gila, 1852."

DISTRIBUTION.—Lower Sonoran of the Colorado Desert, thence into adjacent Arizona, and throughout Lower California to La Paz (BRANDEGEE).

SPECIMENS EXAMINED.—Palm Springs, April 1882, April 18, 1896, April 23, 1907, PARISH 93, 412, 6106; April 10, 1893, DAVIDSON; 1902, F. GILMAN; May 1894, L. D. COPELAND; April 20, 1906, GRANT; May 22, 1911, O. F. SELLIG; July 25–August 14, SCHELLENGER; Indio, May 8, 1903, JONES; McCoy Wash, April 1905, HALL 5946; Borregos Spring, April 19, 1906, JONES; abundant toward the foothills, Mecca, June 28, 1912, PARISH 8133; Old Beach, near Holtville, both above and below sea-level, June 30, 1912, PARISH 8088.

** *Ovules 2, collateral; pod glandular-dotted, exserted; the dead rachises persisting as a spinelike armament. Shrubs, the mature wood glabrous and glandless*

† *Flowers sessile, or nearly so, in open spikes; calyx teeth dissimilar, the lower one narrower and mostly longer than the upper pair; leaves pinnate, or a few of the uppermost simple*

5. **Parosela neglecta,** n. sp.—*Dalea arborescens* Parish, Zoe **4**:341. 1894, non TORREY.—Frutex subspinescens, 1–1.5 m. altus, caulibus junioribus tomentosis, cum glandulis parvis subulatis instructis; foliolis 3–7 oblongis vel obovatis sub tomento canescente obscure glandulosis; spicis 7–15-floris; calyce villoso minute glandulosoque, 8–9 mm. longo, tubo valde nervoso dentes aequante,

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dentibus superioribus duobus acuminatis vel lanceolatis; corolla caerulea, vexillo oblongo-cordato, 8 mm. longo, 4 mm. lato; alis carinaque 6–7 mm. longis; ovario glanduloso-punctato.—Fig. 3.

FIG. 3.—*Parosela neglecta: a*, flowering branch, natural size; *b, c, d*, leaves; *e*, calyx from within; *f*, calyx exterior; *g*, petals; all ×2.5.

In recent years this plant has been taken for *Dalea arborescens* Torr., and in some respects it agrees with the character of that species given in *Plantae Thurberianae*, but is excluded by the phrases "*floribus in spicam densam brevem*

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congestis . . . . spikes ovate or oblong," with which it does not in the least accord.

DISTRIBUTION.—So far as known, local in the neighborhood of Barstow, in the Mojave Desert.

Fishpond Station (Daggett), May 1882, PARISH 644, type; Barstow, May 14, 1897, F. W. HUBBY 141; May 3, 1906, HALL and CHANDLER 6831; May 18, 1905, HALL 6160.

6. PAROSELA JOHNSONII Vail, Bull. Torr. Bot. Club **24**:17. 1897.—*Dalea Johnsonii* Wats., Geol. Expl. 40th Par. **5**:64, 1871.—Shrub 1–1.5 m. high, the slender branches scantily appressed-pubescent or glabrate, glandless or nearly so: leaflets 5–7, linear to narrowly oblong, thinly pubescent and obscurely glandular, narrowed to the rachis: flowers short-pedicellate; calyx sparsely pubescent and nearly glandless, obscurely nerved, 5–5.5 mm. long, the teeth less than half the length of the tube, the upper pair triangular-acute; corolla deep purple; petals about 6 mm. long.

TYPE.—"Near St. George, on the Virgin River, Utah."

DISTRIBUTION.—From southern Utah to the borders of Arizona (Grand Cañon, WILSON) and the eastern border of the Colorado Desert.

SPECIMENS EXAMINED.—Eastern edge of the Colorado Desert, SCHELLENGER; Kane Spring, Ord Mountain, May 1, 1906, HALL and CHANDLER 6826; Cottonwood Mountains, May 11, 1905, HALL 6024.

PAROSELA JOHNSONII (Wats.) Vail var. **Saundersii**, comb. nov. —*P. Saundersii* Abrams, Bull. N.Y. Bot. Gard. **6**:396. 1910; *P. Wheeleri* Heller, Muhlenb. **2**:216. 1906; *Dalea Saundersii* Parish, Bull. S. Cal. Acad. **2**:83. *pl. 2.* 1903.—Leaflets 5–9, lanceolate, sessile, or on short petiolules, glabrate; stems sparsely prickle-glandular.

Victorville, May 12–14, 1903, C. F. SAUNDERS, and May 1905, HALL 6197; Big Pine, Inyo County, May 29, 1906, HALL and CHANDLER 7222; Owens Valley, May 11, 1906, HELLER 8236.

PAROSELA JOHNSONII (Wats.) Vail var. **pubescens**, n. var.—Calycis dentibus majoribus tenuioribusque; legumine pubescente simul glanduloso.

Lee's Ferry, Arizona, June 13, 1890, JONES 3076.

PAROSELA JOHNSONII (Wats.) Vail var. **minutifolia**, n. var.—Foliolis 5–7, oblongis, 2–4 mm. longis.

Mouth Panamint Cañon, May 11, 1906, HALL and CHANDLER 7002; Providence Mountains, May 24, 1905, BRANDEGEE.

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7. PAROSELA CALIFORNICA Vail, Bull. Torr. Bot. Club **24**:17. 1897.—*Dalea californica* Wats., Proc. Am. Acad. **11**:132. 1876.—Shrub 1–2 m. high, hoary with a fine upwardly appressed pubescence, and sparsely beset with prickle-shaped glands: leaves 2–3 cm. long; leaflets 3–7, the terminal often longer than the others, rarely a few simple, the edges thickened, hoary-pubescent, concealing the small glands, decurrent on the rachis or confluent; calyx 5 mm. long, nerved, minutely glandular-dotted, thinly pubescent, in fruit glabrate; teeth shorter than the tube, the upper pair ovate-acute; corolla bright purple; petals 8–8.5 mm. long; pod 8 mm. long; seed castaneous, ovate.—Fig. 4.

Extreme forms, such as Jones's Palm Spring specimen (Hb. U. Cal. 12852), having leaves 3-foliolulate to simple, connect this species too closely with *Dalea Fremontii* Wats., and it is not impossible that it must be reduced to a variety thereof.

TYPE.—"Known as yet only from scanty specimens recently collected by Dr. PARRY in the San Bernardino Mountains, California." According to statements made to the writer by Dr. PARRY, the type was collected east of Banning, on the borders of the Colorado Desert.

DISTRIBUTION.—Western borders of the Colorado Desert, at 150–600 m. altitude, and in the eastern part of the San Jacinto Valley, in the cismontane area.

SPECIMENS EXAMINED.—Near Banning, 1882, PARISH 644, and May 1892, DAVIDSON; Palm Springs, April 1896, PARISH 4111, May 10, 1903, JONES, 1904, R. J. SMITH 308, May 21, 1911, O. F. SELLIG, and May 1902, HALL 1832; Cottonwood Mountains, May 1905, HALL 6025; between Palm Springs and Whitewater, July 25–August 14, E. E. SCHELLENGER, intermediate between the species and the following variety.

PAROSELA CALIFORNICA (Wats.) Vail var. **simplifolia**, n. var.—Glaberrima, ramis eglandulosis: foliis simplicis, rariusve pinnato-3-foliolatis; calycis majoribus.

Western part of the Colorado Desert, 1904, M. F. GILMAN 51 (in Herb. Univ. Cal.).

†† *Flowers pedicellate, in simple racemes; leaves all simple*

8. PAROSELA SCHOTTII (Torr.) Heller, Cat. N. Am. Pl. ed. 2. 6. 1900.—*Dalea Schottii* Torr. Bot. Mex. Bound. 53. 1859.—Compact spinose shrub 1–3 m. high, with numerous slender, green and glabrate, glandless branches: leaves linear, 3–25 mm. long, puberulent, but soon glabrate, bearing near the thickened margins a

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few small, dark, impressed glands: racemes 4–8 cm. long, 6–20-flowered; pedicels 1–1.5 mm. long; calyx 5 mm. long, sparsely hirsute, glabrate in fruit, nerved, and with a row of small red glands,

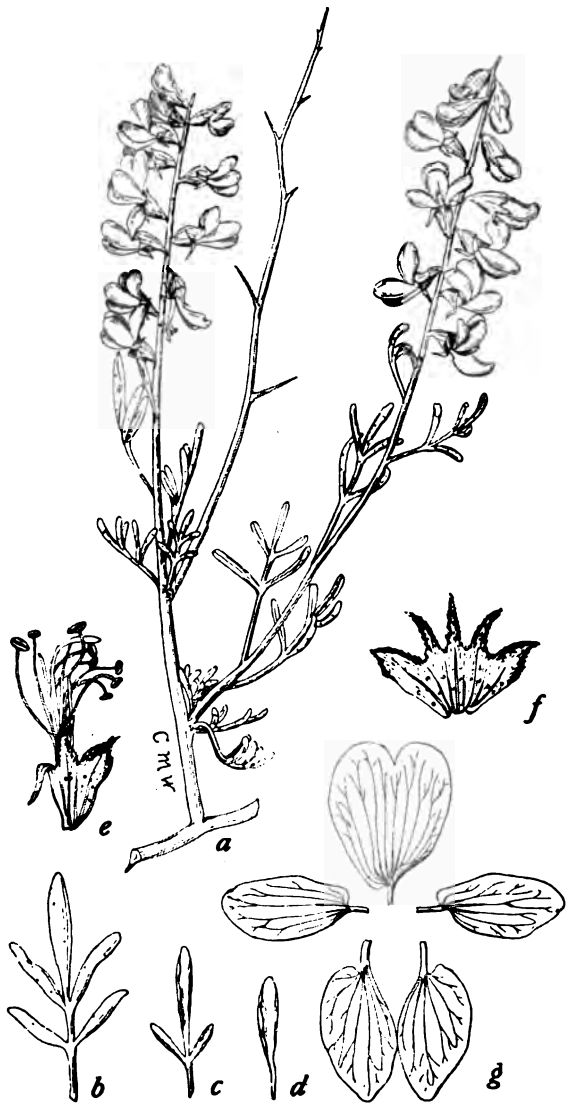

FIG. 4.—*Parosela californica:* *a*, flowering branch, natural size; *b*, *c*, *d*, leaves; *e*, calyx and stamens; *f*, calyx laid open; *g*, petals; all ×2.5.

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very obscure in flower, but distinct in fruit; teeth ciliate, the upper pair a little wider and more obtuse; corolla deep purple; banner 8 mm., wings 10 mm. and keel 8–10 mm. long: pod 1 cm. long, its glands, red: seed castaneous, obovate, 7–8 mm. long.—Fig. 5.

FIG. 5.—*Parosela Schottii:* *a*, flo[illegible] natural size; *b*, calyx; *c*, petals; *a*, pod and fruiting calyx; all ×3.

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Some of the lowest flowers are often in the axils of leaves. The fragrance of the abundant bloom is sometimes diffused for miles on the quiet desert air.

TYPE.—"Diluvial banks of the Colorado, February, SCHOTT."

DISTRIBUTION.—An abundant species of the Colorado Desert, extending into adjacent Arizona and into Lower California (BRANDEGEE).

SPECIMENS EXAMINED.—Palm Springs, April 10, 1880, April 1896, PARISH 83, 4113, April 1904, L. D. COPELAND 4, October 15, 1904, SCHELLENGER 3, 1902, M. F. GILMAN 21, April 1905, HALL 5738, and May 21, 1911, O. F. SELLIG; Coachella, April 1905, GREATA and HALL 5781; Chuckawalla Mountains, April 1905, HALL 5973; Indio, April 1905, HALL 5990.

PAROSELA SCHOTTII (Torr.) Heller var. **puberula,** n. var.—Rami juvenes foliaque canescente puberuli; calyce parum vel dense pubescente.

Colorado Desert, April 1905, BRANDEGEE; Borregos Spring, April 29, 1904, BRANDEGEE; Cajon de Santa Maria, Lower California, May 10, 1889, BRANDEGEE.

*** *Ovules 4 (-6); calyx teeth similar, pod glandular-dotted, exserted; flowers spicately scattered on stout spine-tipped branchlets* (*Asagraea* Baillon, Adansonia **9**:232. 1870)

9. PAROSELA SPINOSA Heller, Cat. N. Am. Pl. ed. 2. 7. 1900.—*Dalea spinosa* Gray, Mem. Am. Acad. **5**:315. 1855; Torrey, Pac. R.R. Rep. **7**[3]:9. *pl. 3.* 1856; *Asagraea spinosa* Baillon, Adansonia **9**:233. 1870.—Intricately branched tree 4–7 m. high, the numerous spinescent branchlets hoary with a fine close pubescence, and sparsely dotted with small flat glands; leaves very few and promptly deciduous, narrowly oblong, the margins thickened, 5 mm. long: flowers on pedicels 1 mm. long; calyx 5 mm. long, strongly nerved, encircled above with a ring of large, reddish, guttate glands; teeth 2 mm. long, ovate; corolla dark blue; banner 6 mm. long and as broad; keel and wings 8 mm. long; anthers with an oblong red gland at base.

The flowers do not extend to the sharp horny spine of the branchlets, not all of which are floriferous, and which cannot be regarded as the peduncles of a true spicate inflorescence. *Parosela Kingii* (Wats.) has solitary flowers borne on like spinescent branchlets, and *Holocantha Emoryi* Gray has an analogous inflorescence.

TYPE.—"Arroyos on the Gila; and on the California Desert west of the Colorado."

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DISTRIBUTION.—At low altitudes in the Colorado Desert, thence to adjacent Arizona, Sonora, and Lower California.

SPECIMENS EXAMINED.—Colorado Desert, 1894, A. W. ANTHONY; Whitewater, May 1904, R. G. SMITH; Palm Springs, June 1895, DAVIDSON, in full flower, and April 1907, PARISH; Chuckawalla Bench, June 25, August 14, 1903, SCHELLENGER 2, 3; Indio, June 1880, PARISH 22; toward the foothills near Mecca, and in Red Cañon, abundant and in full bloom, June 28, 1912, PARISH 8108.

SPECIES INCERTA

DALEA ARBORESCENS Torr. ex Gray, Mem. Am. Acad. II. 5:316. 1885.—"Much branched, almost glandless, subspinescent; the adult branches glabrate, the younger, together with the leaves and the calyces, canescent-tomentose: leaflets 5, approximate, obovate: flowers congested in a short dense spike; bracts small, subulate; the acuminate teeth of the calyx as long as the campanulate tube, the two upper oblong-triangular, the others narrowly lanceolate: petals (purple?) about equal.

"'A small tree!' Glands scarcely any, a few minute tubercular ones occasionally found on the branchlets when denuded of their dense woolly covering. Leaves petioled, the leaflets only 2–3 lines long. Flowers 5–6 lines long; the calyx large in proportion, the tube obscurely striate. Vexillum obcordate."

The above is the original character, the first paragraph translated. The type is said to be from the "Mountains of San Fernando, a southern branch of the Sierra Nevada, California; April, FREMONT." This region is now well known, but no species of *Parosela* has been collected there; certainly it could hardly have escaped notice if a tree. The type specimen is a mere fragment, from which little can be learned. The condensed inflorescence indicates that it should be placed near *Parosela polyadenia* and *P. Emoryi*, where it was located by WATSON in the *Botany of California*.

SAN BERNARDINO, CAL.

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THE EFFECT OF SOME PUGET SOUND BOG WATERS ON THE ROOT HAIRS OF TRADESCANTIA

GEORGE B. RIGG

The theory advanced in this paper is that plants other than bog xerophytes are excluded from peat bogs because of their inability to produce normal root hairs in the toxic habitat of bogs, their absorptive surface being thus so decreased that they cannot get water enough to enable them to live. The writer has also confirmed with Puget Sound bog waters certain results obtained by other workers with bog waters from the Middle West and extreme East.

Description of bogs

The xerophilous character of the flora of peat bogs is well known. In the Puget Sound region the plants most characteristic of undrained bogs are *Ledum groenlandicum*, *Kalmia glauca*, *Oxycoccus oxycoccus intermedius*, *Sphagnum*, and *Drosera rotundifolia*. The first four plants named are found in every undrained bog that the author has visited in the region, while the last one has been found absent from a few. Other plants sometimes found in bogs of the region are *Pinus monticola*, *Betula glandulosa*, *Salix myrtilloides*, *Myrica Gale*, *Eriophorum russeolum*, and *Juncus oregana*. *Tsuga heterophylla* and *Pinus contorta* are found on the drier hummocks in bogs (**8**), *Ledum columbianum* and *Myrica californica* are reported to be found in the beach bogs along the Pacific Ocean instead of *L. groenlandicum* and *M. Gale* (**8**).

Peat bogs are common in the Puget Sound region. The studies reported in this paper are based on six bogs. One of these is situated within the city of Seattle at the corner of E. 55th St. and 6th Ave. N.E. During the last two years the forest surrounding this bog has been cleared away and the streets along its edges have been filled with dirt from the neighboring hills. It has not been drained however and its flora is still just as typical as it was before the surrounding forest was removed, except that *Drosera*

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rotundifolia has disappeared, which was fairly common in this bog in 1908. It is a small bog, about 100 by 200 m. in extent. For convenience it will be referred to as the Seattle bog.

The largest bog studied is situated about 1760 m. east of Henry Station on the Seattle-Everett interurban railway. The undrained portion of this bog is perhaps 16 hectares in area, and its flora is typical, including *Drosera*. In addition to the usual bog plants, *Pinus monticola* is common, and *Trientalis arctica* is found along the border. The natural contour of the region is such that there is some drainage from the northern end of this bog into a small creek, and that portion of it lacks *Drosera* and *Pinus* and has *Lysichiton kamtschatcense*. This bog will be referred to as the Henry bog.

The bog situated about 5280 m. southeast of Fauntleroy Park in Seattle is a little smaller than the Henry bog. Its area is estimated at about 10 hectares. *Drosera* is abundant in it, and *Trientalis arctica* is common along its margin. This bog will be designated as the Fauntleroy bog.

The bog situated at Echo Lake station on the Seattle-Everett interurban railway is slightly smaller even than the Seattle bog. It is on the margin of Echo Lake and its edge forms the bank of the lake for a short distance. The bog flora is typical right up to the open water of the lake; *Drosera* is abundant, and *Comarum palustre* is found on the border of the lake immediately adjacent to the bog. This bog will be called the Echo Lake bog. It is about 8800 m. distant from the Henry bog.

The bog that will be referred to as the Green Lake bog is situated just north of the city limits of Seattle. It is a little over 1760 m. north of Green Lake, which is entirely within the city limits. There is now remaining only about 0.4 hectare of this bog; formerly it was about 12 hectares in extent, but nearly all of it has been stripped of its original vegetation and drained. A good deal of it has been divided into small garden tracts and some of these are now under cultivation. The uncleared portion is drained by roadside ditches on two sides; water flows freely from the bog into one of these ditches during the rainy season and there is considerable seepage into the other one. This bog still has the typical bog

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plants of the region, including *Drosera*. In addition to these, however, it contains the following plants not usually found in bogs: *Pseudotsuga taxifolia*, *Picea sitchensis*, *Thuja plicata*, *Tsuga heterophylla*, *Alnus oregona*, *Comarum palustre*, *Lysichiton kamtschatcense*, a *Carex*, and a small orchid. It will be noted that some of them (e.g., *Lysichiton kamtschatcense*) are found on the borders of other bogs, and that one of them (*Tsuga heterophylla*) is found on the dry hummocks in other bogs. Apparently the partial drainage here has allowed the entrance of plants not found in typical bogs, but has not driven out the typical bog plants.

The last of the six bogs is situated on Mount Constitution at an elevation of about 666 m.; the mountain itself attains a height of 880 m. It is situated on Orcas Island, one of the San Juan group, which lies between the strait of Juan de Fuca and the strait of Georgia. Several peat bogs situated on this mountain have been drained and thus converted into meadows, which have been used for both hay and pasturage. Drainage and clearing seem to have completely destroyed the bog flora and substituted a flora not at all characteristic of peat bogs.

The bog water for use in the experiments has been obtained in all cases as follows. Care was first taken to select a spot that was centrally located in the bog and had a typical bog flora. The mass of vegetation and fibrous peat was cut away with a strong knife from an area about one foot square. Then the soft peat was scooped out below this until a cavity was formed that would soon fill with water. The water was dipped up in a wide-mouth glass bottle and poured into glass containers. The depth to which this had to be scooped out varies with the season; in winter about 35 cm. sufficed in most of the bogs; in late summer it was necessary to dig 90 cm. In the case of the water obtained from the Henry bog on October 10, 1911, it was found that it would not accumulate in half an hour by digging even 90 cm. deep, and a glass jar was filled with very wet peat and the water was squeezed through cheesecloth in the laboratory.

The tap water used was that supplied to the laboratories from a wooden supply tank on the University campus. It is pumped into this tank from Lake Washington.

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The expression "normal root hairs" used in this paper with reference to *Tradescantia* (the species common in greenhouses, and known as wandering Jew) means such root hairs as grow on the roots of cuttings in tap water. These hairs cover the entire surface of the root even when it reaches a length of 70 mm. or more. They are almost uniformly distributed, 4 mm. or more in length, mostly straight, and appear to the naked eye like somewhat silky fibers. Over 200 specimens of this plant grown in tap water have been examined and there has been found practically no variation from this description.

Investigation

In October 1909 experiments were begun on the germination of wheat, corn, beans, and peas in moist peat and between sheets of moistened blotting paper. It was found that these seeds germinated just as readily when the moisture was furnished by bog water as when it was furnished by tap water.

In the fall of 1910 *Ledum groenlandicum* and *Kalmia glauca* were propagated by cuttings in both bog water and tap water in the laboratory. Young roots from both of these species from both kinds of water were examined and found to be entirely devoid of root hairs. Some of the roots examined were produced on old roots formed before the plants were removed from the bog and some were produced on stems.

TRANSEAU (10) found root hairs absent in *Oxycoccus macrocarpus*. He also found that the roots of *Larix laricina* were "composed of mycorhiza," and that their cortical tissues were early destroyed by a fungus. When he grew these plants in a well-aerated culture solution "normal roots with root hairs were produced."

COVILLE (1) found *Vaccinium corymbosum* to be devoid of root hairs. He found also that the walls of the epidermal cells of the roots were 1.3–2.5 μ thick, this being four to six times as thick as the walls of epidermal cells of wheat roots. He computes that a given section of wheat root presents about ten times as much absorptive surface as a section of blueberry (*Vaccinium corymbosum*) root of the same area.

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In the fall of 1909 and again in 1910–1911 experiments were conducted on the effect of bog water on the production of root hairs on cuttings of *Tradescantia*. The experiments reported in the following table were carried out in 1910–1911 in 150 cc. glass bottles with extra wide mouths.

TABLE I

THE PRODUCTION OF ROOT HAIRS ON TRADESCANTIA IN BOG WATER

	No. of plants used	Root hairs			
		Normal	Slightly stunted	Much stunted	None
Seattle bog	16	..	3	9	4
Henry bog	10	..	1	9	..
Fauntleroy bog	10	..	3	6	1
Echo Lake bog	5	..	..	2	3
Green Lake bog	10	10	..	..	..
Mount Constitution bog	3	..	..	3	..

It will be noted that the Green Lake bog is the only one whose water allowed the production of root hairs that were normal as to length and abundance. It seems evident that this lack of toxic effect is a result of drainage. Of the 44 plants grown in water from undrained bogs, 8 plants (18 per cent) produced no root hairs, while 29 plants (66 per cent) produced root hairs that were much stunted, and 7 plants (16 per cent) produced root hairs that were slightly stunted.

The above table is based on the roots produced within the first 14 days; these roots were invariably shorter than those produced in tap water within the same time. The new roots that started after that time approximated the length of the roots of plants grown in tap water and produced root hairs that were longer and much more abundant, in many cases approximating normal. The tops of the bottles in which these experiments were carried on were not closed, the surface of the water being exposed freely to the air. DACHNOWSKI (2) found that aeration reduced the toxic effect of bog water from Cranberry Island (Ohio).

In addition to the tests made on bog water and tap water the following tests have been made on other waters of the region: Echo

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Lake (5 plants), bog spring on Mount Constitution (3 plants), Mud Lake (10 plants), well water at Friday Harbor, Washington (25 plants). In every one of these cases the root hairs were normal. The water from Echo Lake was dipped up by the writer while standing on the edge of the Echo Lake bog; it was obtained at a distance of 15 feet from where the water from the Echo Lake bog was obtained. The bog spring on Mount Constitution referred to emerges from the side of the mountain and its water seeps into the swamp which gradually merges into the bog. It has the coffee color characteristic of bog water, but not to so marked a degree as the water obtained from underneath typical bog vegetation.

Mud Lake is so close to Lake Washington that the two are connected during the winter season. It is a circular lake about 880 m. in diameter. There is some bog vegetation near its southern end, and the situation of this vegetation appears to be in a general way similar to that of Buckeye Lake bog in Ohio described by DACHNOWSKI (5). The water used was obtained from the edge of the lake at a distance of 90 m. or more from the bog vegetation. The well water used at Friday Harbor was obtained from a surface well near the Puget Sound Marine Station. This is called "tap water" in table I, since the effect of the two has been found to be identical.

Plants were also grown in several solutions which it was expected would prove toxic. The following list of substances was found to produce stunting of the root hairs of *Tradescantia* of an amount and kind comparable with the effect of undiluted bog water: sea water diluted with three times its volume of tap water; carbolic acid, 0.001 per cent; formalin, 0.001 per cent; gelatin, 0.001–0.002 per cent; tea; coffee. In undiluted sea water no roots developed. Stronger solutions of carbolic acid and of formalin entirely inhibited the development of roots.

It is of course possible that formalin might develop from the slow decay of woody materials in the bog in the absence of oxygen, but I have not found any evidence of its presence in bog water. We might reasonably expect, also, that tannin would be found in bogs, but we have no direct evidence that it is a factor in limiting bog floras.

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The effect of dilution with tap water was tried with the results shown in the following table:

TABLE II

THE EFFECT UPON ROOT HAIRS OF TRADESCANTIA OF BOG WATER DILUTED WITH TAP WATER

Bog	No. of exp.	Amount of dilution	Root hairs			
			Normal	Slightly stunted	Much stunted	None
Seattle bog.....	1	$\frac{3}{4}$	1	..	..	..
Seattle bog.....	11	$\frac{1}{2}$	11	..	..	..
Henry bog.....	10	$\frac{1}{2}$	7	3	..	..
Fauntleroy bog	10	$\frac{1}{2}$	10	..	..	..
Fauntleroy bog	5	$\frac{1}{4}$	5	..	..	..
Fauntleroy bog	10	$\frac{1}{10}$	..	5	4	1

From this it appears that the toxin is present in such small amounts that slight dilution greatly decreases the toxic effect. This is in line with the results obtained by LIVINGSTON (7) on *Stigeoclonium*.

Three samples of water from the Henry bog were boiled until each was reduced to one-eighth of its original volume. *Tradescantia* cuttings were placed in them. Few roots started, no root hairs were formed on them, and the plants soon died.

The effect of filtering bog water from the Henry bog through filter paper was tried. The water was collected on October 10, 1911, and three plants were grown in it. They all produced normal roót hairs.

A preliminary investigation was made as to the presence and activities of bacteria in the Seattle bog and the Henry bog. Briefly the results may be stated as follows.

1. Beans, peas, and corn decay just as readily in bog water as in tap water.

2. Fresh beef decays a little more slowly in bog water collected in a sterilized jar and kept sealed than it does in tap water under the same conditions.

3. The amount of difference in the rate of decay of pieces of fresh beef buried in bogs and of other pieces buried in swamps is very slight, it being a little more rapid in swamps.

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4. Bacteria were found in every case in both bog water and peat collected under sterile conditions. Some of the specimens of peat were collected from as great a depth as 75 cm.

5. *Bacillus subtilis* and *Pseudomonas liquefaciens* were identified in cultures made from surface waters in the Seattle bog.

TRANSEAU (9) found bog waters to be teeming with bacteria. DACHNOWSKI (4, 5) has found bacteria abundant and has given his attention largely to their physiology. Apparently the position that bog waters are very strongly antiseptic is no longer tenable.

Discussion

Suggestions offered by three other investigators (LIVINGSTON, DACHNOWSKI, and COVILLE) bear on the theory stated at the beginning of this paper. In 1905 LIVINGSTON (7) concluded that there were chemical substances present at least in some bog waters that affected the alga that he used (*Stigeoclonium*) as did poisoned solutions, and that these substances are not related directly to the acidity of the water. He concludes that "the stimulating substances here demonstrated may play an important rôle in the inhibition from bogs of plants other than those of xerophilous habit." In 1909 DACHNOWSKI (3) stated his belief "that there are present in bog water and in bog soils injurious substances which are, at least in part, the cause of xerophily in plants and of decreased fertility in bog soils." In 1910 COVILLE (1) stated that "the swamp blueberry (*Vaccinium corymbosum*) grows in peaty soils which contain acid or other substances poisonous to plants. As a protection against the absorption of amounts of these poisons great enough to prove fatal, this plant, like many other bog and acid-soil plants, is devoid of root hairs and consequently has a restricted capacity for absorbing soil moisture." In 1911 DACHNOWSKI (5) words his theory a little differently and speaks of "the toxicity of the habitat and its consequent physiological aridity and selective operation on forms striving for occupancy." In the same paper DACHNOWSKI says that "the reduced absorptive capacity of the plants is not a consequence of the absence of root hairs or of a smaller absorbing surface."

It is thus seen that LIVINGSTON suggested that bog toxins

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excluded certain plants from bogs, but did not express any opinion on root hairs, while COVILLE stated the theory that certain plants were devoid of root hairs as a protection against bog poisons, but does not give an opinion whether the bog habitat as it at present exists caused the loss of these root hairs. Neither does he express any opinion as to how mesophytic plants are kept out of bogs. It is to be borne in mind that COVILLE was working on a specific economic problem and evidently did not concern himself, in the paper quoted, with questions of pure science. DACHNOWSKI at first thought that toxins caused xerophily in bog plants and later that the toxicity caused bogs to exercise a selective operation, but does not suggest any injurious effect of bog toxins on root hairs as the cause of such selective operation.

TRANSEAU'S work (10) would seem to suggest that *Larix laricina* is adapted to the Michigan bogs because it can still live after the loss of its root hairs and even after the destruction of the cortical tissues of its roots. *Larix*, however, is not a genus that is universally characteristic of bogs as are such genera as *Ledum*, *Kalmia*, *Oxycoccus*, and *Vaccinium*. There seems to be room for doubt as to the cause of the death of the root hairs and of the cortical tissues of the roots of *Larix* in the Michigan bogs. It is possible that they may be killed by a toxin and attacked by a saprophytic fungus afterward. It is also possible that they may have been killed by a parasitic fungus.

Definite conclusions as to the relation of the toxicity of the bog habitat as a cause and the stunting of root hairs as a result cannot, of course, be drawn from the results obtained from the use of water from six bogs on a single species. Further work must be done with other bog waters and other plants to show how far these two things are related as cause and effect. The question of how bog plants came to be devoid of root hairs is quite a different question from that as to why mesophytic plants are now excluded from undrained bogs. DACHNOWSKI, who in 1909 (3) believed in the activity of bog toxins in causing xerophily in bog plants, states (5) in 1911 that "during the glacial period most species common to bogs skirted the ice sheet." Whether these plants were under bog conditions at this time or whether their distribution was related

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to low temperatures only does not seem to be settled. Evidently extremely low temperatures must be reckoned with as one of the factors that determine the characteristics of these plants in past ages, and the same is true of bog plants growing in the extreme north in post-glacial times. We certainly are not justified in concluding that bog conditions as they exist today in temperate regions are the cause of xerophily in bog plants. There does seem to be ground for the belief that certain plants having hairless roots and other xerophilous structures are able to live in bogs, while other plants that normally have root hairs and possess in general a mesophytic or tropophytic structure are kept out of the bogs by these toxins.

It now seems well established that the inhibition from undrained bogs of plants other than xerophytes is not caused by acidity as such (H ions) (LIVINGSTON 7), nor by low osmotic pressure (LIVINGSTON 6), and that it cannot be correlated with low temperatures or strong drying winds (DACHNOWSKI 5), or directly with lack of aeration. Although the toxic effect of bog waters does disappear with continued aeration (DACHNOWSKI 2), it seems evident that the presence of air destroys the toxic substances that are present in bog water, and that the mere absence of air from water does not render it toxic. The fact that DACHNOWSKI (5) found that the toxic effect of bog water can be removed by filtering it through agricultural soils and that the toxic effect was then present in the soil used as a filter seems to settle the point. Whether the toxic effect of bog waters is due to one substance or to several we do not know. Nor do we know positively that it is always due to the same substance or mixture of substances. Undoubtedly the toxic substances are organic, and the problems of organic analysis involved are beyond us at present.

What the source of the toxin (or toxins) is we do not know definitely. There seem to be at least three possible sources: (*a*) excretion products coming into the substratum from plants growing in the bog, (*b*) products resulting from decay in the absence of oxygen, (*c*) excretion products of bacteria. Since it is probable that many other fungi are associated with the bacteria in bogs, it seems scarcely possible to distinguish sharply between (*a*) and (*c*).

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Since *Sphagnum* is the one macroscopic plant always present in bogs, our attention would naturally be directed to that. Since the presence of *Sphagnum* and the lack of drainage are the two conditions necessary for the formation of bogs, it seems probable that in this combination is the place to seek for the production of the toxin. Bacteria, however, seem to be always present in bogs and their excretion products are to be taken into account.

DACHNOWSKI (5) finds reason for believing that bacteria are active agents in enabling peat bogs to admit certain plants and exclude others. As the same investigator (4) has suggested, the large number of chemical and biological agents present may react collectively with the results of decomposition. Since it has been found by DACHNOWSKI (3) that the presence of a considerable amount of a finely divided insoluble substance destroys the toxic effect of bog water, it seems possible that the absence from bogs of ordinary insoluble soil substances may be a factor in the production of toxicity in bogs.

DACHNOWSKI (5) has given recently a historical summary of the theories of the causes of the xerophilous character of bog plants. In this summary he says "LIVINGSTON suggests the presence of chemical substances not in direct relation to the acidity of the soil as acting on the vegetation. Another explanation, that of the toxicity of the habitat and its consequent physiological aridity and selective operation upon forms striving for occupancy, has been offered by the writer of this paper." In the paper above quoted LIVINGSTON says "the result of these tests is, briefly, that many bog waters act upon the plant [*Stigeoclonium*] like *poisoned* solutions." Again, he says "diluting the . . . . samples . . . . with distilled water or with a weak nutrient solution decreases the *toxic* effect." In his summary he says "the *stimulating* substances here demonstrated may play an important rôle in the inhibition from bogs of plants other than those of xerophilous habit."

It seems to the writer that the toxin theory of the cause of the exclusion from bogs of plants other than certain xerophytes originated with LIVINGSTON. The theory has been greatly extended and a wealth of experimental data given to support it by DACHNOWSKI,

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and the present paper contributes the suggestion that the toxins act through their stunting effect on root hairs.

The bog problem was suggested to the writer by Professor THEODORE C. FRYE, of the University of Washington, and he has had the advantage of his criticism and advice as well as that of Dr. JOHN WEINZIRL, bacteriologist in the same department.

Summary

1. *Tradescantia* grown in bog water shows stunted root hairs.

2. *Tradescantia* grown in water from open lakes and springs immediately adjacent to bogs shows normal root hairs.

3. *Tradescantia* grown in water from drained or partly drained bogs shows almost normal root hairs.

4. The stunting of root hairs of *Tradescantia* by bog water is comparable with the stunting of them by exceedingly dilute solution of sea water, of formalin, of tannic acid, of gelatin, of coffee, and of tea.

5. The stunting effect of bog water on root hairs of *Tradescantia* disappears when it is diluted with an equal volume of tap water and in some cases when diluted with one-half its volume of tap water.

6. The stunting effect of bog water on root hairs of *Tradescantia* may be increased by boiling the water down to a fraction of its original volume.

7. Many typical bog plants have no root hairs.

8. There seems to be a toxin or toxins in bog water whose effect disappears with drainage of the bog.

9. Possibly this toxin inhibits mesophytes from bogs by reducing the amount of absorptive surface exposed by the root system.

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8. PIPER, C. V., Flora of Washington. 1906.
9. TRANSEAU, E. N., The bogs and bog flora of the Huron River Valley. BOT. GAZ. **40**:351–375. 1905.
10. ———, The bogs and bog flora of the Huron River Valley. BOT. GAZ. **41**:17–42. 1906.

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CURRENT LITERATURE

BOOK REVIEWS

The ecology of water plants

Long ago the ecological features of the hydrophytes were brought together in comprehensive fashion by SCHENCK in two admirable volumes. Recently Dr. HUGO GLÜCK, a young and enthusiastic investigator, has published three volumes along similar lines, and they are very rich in detailed information; indeed, they may be regarded as encyclopedic in nature. The first two volumes, dealing respectively with the European Alismaceae and the genus *Utricularia* (together with an account of turion formation), have been noticed in these pages.[1] The third and thus far the largest volume, which is now at hand, is very different in scope, treating as a whole the vegetation of fresh-water banks, that is, the marginal vegetation of streams and ponds.[2] This vegetation is essentially that of the belts which are subject to inundation, and embraces, therefore, practically all of the so-called amphibious plants. These plants, of course, are among the most interesting of all plants to ecologists because of their plasticity.

While most of the genera and many of the 124 species treated in this volume are of very widespread distribution, the author limits his studies to central and southern Europe. The work is based on almost numberless field trips to all parts of this vast region, and these observations have been backed up by numerous cultures. The author makes no pretense to completeness, suggesting, indeed, that these are among the most poorly known of all plants, and that they are well worthy of much more careful study; some color is given to this view by GLÜCK's discovery, in these floristically best known of all lands, of entirely new areas for four different species. The author recognizes two "zones" (thus ignoring the Brussels recommendation of 1910 that the term zone be employed henceforth only for the great climatic belts of the earth), one of the land margin with leaves mostly aerial, and one of the water margin with leaves mostly submersed. The subdivision of the "zones" into groups and subgroups is based not on habitat but on leaf form. For example, "zone 1" includes a group with linear leaves (as *Typha*, *Acorus*, *Iris*), a group with petioled entire leaves, a group with petioled divided leaves, etc. Under each group or subgroup the species are considered individually, and under each

[1] BOT. GAZ. 43:67–69. 1907.

[2] GLÜCK, HUGO, Biologische und morphologische Untersuchungen über Wasser- und Sumpfgewächse. III. Die Uferflora. pp. xxxiv+644. *pls. 8. figs. 105.* Jena: Gustav Fischer. 1911.

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species there is usually a further subdivision into such topics as land form, water form, submersed form, form with floating leaves, etc. The greater part of the work is taken up by the plants of the water margin ("zone 2"). These belong to two categories, so far as leaf form is concerned, those that are homoblastic or with but one leaf type, and those that are heteroblastic or with two leaf types; the heteroblastic water plants are with us well represented by such plants as *Sium* and *Proserpinaca*. Most of the plants of "zone 1" have greatly reduced water forms, many of which are generally unfamiliar, and some of which are known only from cultures; these forms rarely flower. One of the striking discoveries is a water form of a dodder (*Cuscuta alba*) which parasitizes *Isoetes* and water buttercups. Only a few of the species studied live in flowing water. The water forms seem related to low temperatures, and while the land form is essentially a summer form, it can sometimes be produced at other seasons by raising the temperature of the cultures. Most of the species have winter rest periods, but there are some species that vegetate continuously, even in countries with cold winters. Many Mediterranean species have periods of summer rest. These and many other topics are considered in the 40-page summary with which the volume concludes. The book should be in every botanical reference library, for it will serve as a compendium of general ecological information about the plants it treats. It is understood that Dr. GLÜCK is devoting his life to the study of water plants, and we may expect other volumes of this sort in the future.—HENRY C. COWLES.

Plant breeding in Sweden

The extensive series of experiments in plant breeding which have been conducted in Sweden, principally at the Svalöf station, beginning about 1886 and extending with ever increasing efficiency to the present time, are of great interest not only to agriculturists but also to scientists by reason of the problems of inheritance which they involve. Unfortunately very scanty reports of these operations have been available in any but the Swedish language, and these publications have been, and quite rightly so, most largely concerned with practical results that were of special interest to the farmers of Scandinavia. These circumstances will make the present report[3] the more useful, prepared as it is by one who has carefully investigated the methods employed and the results obtained at the Swedish stations, and addressed primarily to the scientific reader, but in language intelligible to the general public.

The report contains a brief historical sketch of the inception and development of plant breeding experimentation in Scandinavia, examples of the experiments with different agricultural plants, some of the results obtained, and a summary of the principles now recognized by the plant breeders at Svalöf and followed in their work. These principles are briefly: (1) the recognition

[3] NEWMAN, L. H., Plant breeding in Scandinavia. 8vo. pp. 193. *figs. 63*. Ottawa, Canada: Canadian Seed Growers' Association. 1912. $1.00.

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that a progressive system of plant improvement cannot be a one-sided system, but must embrace all possible methods of reaching the desired end; (2) artificial hybridization provides an invaluable means of obtaining characters in superior combinations which do not occur in nature and this method is now largely used at Svalöf for this purpose; (3) the old system of "mass selection" can still be of value in special cases and has never been fully abandoned; (4) instead of basing the isolation of superior individuals (or lines) purely upon botanical or morphological characters, as was formerly done, the principle has become to select a large number of individuals without special regard to such characters, the valuation of these individuals (or lines) to rest upon tests conducted with the greatest care and extending over a series of years. This means the recognition of the importance of physiological as well as morphological unit characters, and the abandonment of reliance upon the use of correlation of characters as any important aid in estimating the practical value of an individual or line.

Detailed reports of some investigations, some sixty illustrations from drawings and photographs, and a comprehensive bibliography add to the value of the volume. Dr. TEDIN, specialist for barley at Svalöf, says of the book: "The exposition is pertinent and correct and thereby distinguishes itself from practically all accounts hitherto written in a foreign language."—GEO. D. FULLER.

The cotton plant

W. LAWRENCE BALLS, "cryptogamic botanist" on the staff of the Khedivial Agricultural Society, has published a volume on the cotton plant in Egypt.[4] It brings together information of the most varied character, the material being assembled as if to "take account of stock" preliminary to a fuller monograph. The four sections of the book treat of the history of cotton in Egypt, the individual plant, the race, and the economics of cotton, the second and third sections being of special interest to botanists.

In the account of "the individual plant" a brief outline of fertilization (including the conspicuous cytological features) and embryology is given (8 pp.), followed by an account of experimental work on "development and environment" (67 pp.). This physiological work includes such topics as germination conditions, temperature and growth, effect of sunshine, night temperatures, hypocotyl and root growth, transpiration (including its relation to stomata), tissue temperatures, photosynthesis, the growth curve, the flowering curve, etc. The cotton fiber of course is described in detail (8 pp.). In the account of "the race," the problems of fluctuation, commercial varieties, natural crossing, and heredity are presented (87 pp.), quite a number of graphs presenting to the eye the results of much experimental work.—J. M. C.

[4] BALLS, W. LAWRENCE, The cotton plant in Egypt; studies in physiology and genetics. pp. xvi+202. *figs. 71.* London: Macmillan & Co. 1912. 5 *s.*

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Tree manuals

Among the many books upon various phases of tree study two recently to hand seem well suited to the use for which they were intended. The first[5] includes the native and cultivated woody plants of Minnesota, and in its semitechnical nature is intended to appeal to the educated layman quite as much as to the teachers and students of botany and forestry. This appeal is the more readily made through the numerous excellent illustrations, both from drawings and photographs.

In the second manual[6] the same classes are appealed to, and in addition to simplicity of text and abundance of excellent illustrations, the book has further to recommend it, its pocket-size, which allows it to be most conveniently carried into the forests themselves. The leather covered edition is in fact the best and most portable small tree manual that has yet appeared. —GEO. D. FULLER.

MINOR NOTICES

A sketch of Linnaeus.—Professor EDWARD LEE GREENE[7] has published an admirable sketch of LINNAEUS, which the publishers have presented in most attractive form. The personality of this great Swede should live beyond the circle of professional taxonomists, and the simple and fine style of this sketch makes the booklet a most effective one for the teachers of public schools and for reading circles. The nine sections deal with the following topics: lineage and childhood of LINNAEUS; school, college, and university years; journey to Lapland; journey to Germany and Holland; practices medicine in Stockholm; appointed professor at Upsala; influence of LINNAEUS upon botany; LINNAEUS as a zoologist (contributed by W. H. DALL); LINNAEUS as an evolutionist. These sections introduce LINNAEUS the man rather than as the father of taxonomy, and a most interesting and inspiring man he proves to be. We are told of his parentage and early education, of his struggles with adverse circumstances, and of the almost incredible patience, industry, zeal, and resolution with which he conquered and rose to high distinction. No one could introduce him more intelligently, sympathetically, and in better form than Professor GREENE.—J. M. C.

Indiana Academy of Science.—The Proceedings of the Indiana Academy of Science for 1911 (1912), a volume of 473 pages, contains the following botani-

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[5] CLEMENTS, F. E., ROSENDAHL, C. O., and BUTTERS, F. K., Minnesota trees and shrubs. Report of the Botanical Survey IX. 8vo. xxi+314 (illustrated). Minneapolis, Minn.: University of Minnesota. 1912.

[6] COLLINS, J. F., and PRESTON, H. W., Illustrated key to the wild and commonly cultivated trees of the northeastern United States and adjacent Canada. vii+184. *figs. 279.* New York: Henry Holt & Co. Cloth $1.35; leather $2.50.

[7] GREENE, EDWARD LEE, Carolus Linnaeus. pp. 91. Philadelphia: Christopher Sower Company. 1912.

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cal papers: Some variations in plants, by F. M. ANDREWS; Report of the work in corn pollination (III), by M. L. FISHER; New and notable members of the Indiana flora, by E. J. GRIMES; A monograph of the common Indiana species of *Hypoxylon*, by CHARLES E. OWENS; The improvement of medicinal plants, by F. A. MILLER; Nutrients in green shoots of trees, by E. J. PETRY; The New York apple tree canker, by LEX R. HESLER; Value of fertilizing constituents of weeds of Indiana; analysis of ironweeds, by FRANK MATHERS and Miss GAIL M. STAPP; The prevalence and prevention of stinking smut in Indiana, by C. T. ORTON; Indiana fungi (II), by J. M. VAN HOOK; Diseases of ginseng caused by Sclerotinias, by GEO. A. OSNER; Additions to the flora of the Lower Wabash Valley (by Dr. J. SCHNECK), by CHARLES C. DEAM; Plants new or rare in Indiana, by CHARLES C. DEAM; The unattached aerial forms of plant rusts in North America, by A. G. JOHNSON.—J. M. C.

Sylloge Fungorum.[8]—Volumes XIX and XX of this extended work, bearing the subsidiary title *Index Iconum Fungorum*, contains a bibliographical index to illustrations of fungi, and includes references to works of many of the early as well as the more recent authors. References to illustrations are indicated briefly but clearly; synonyms are introduced frequently and serve as a ready and unmistakable means of cross reference. Volume XIX enumerates alphabetically the genera *Abrothallus* to *Lysurus* inclusive, and Volume XX continues with *Macowanites* to *Zythia*. The species under their respective genera and the bibliographical references thereto are likewise in alphabetical sequence, and the terminology is in accordance with the international rules of botanical nomenclature. The amount of detailed and painstaking labor involved in the achievement of such a task is enormous, but the final result in this case is a valuable work of reference, indispensable to the mycologist and helpful to the general student of botany.—J. M. GREENMAN.

NOTES FOR STUDENTS

Current taxonomic literature.—C. A. DARLING (Torreya **12**:155–164. 1912) has issued a "Key to the wild and cultivated trees in autumn." The key is intended for use in the field for the identification of trees occurring in eastern United States.—A. DAVIDSON (Bull. So. Cal. Acad. Sci. **11**:77. *pl. 1.* 1912) describes and illustrates a new species of *Frasera* (*F. puberulenta*) from California.—B. O. DODGE (Mycologia **4**:218–222. *pls. 62, 63.* 1912) describes and illustrates a new species of *Ascobolus* (*A. magnificus*) from artificial cultures

[8] SACCARDO, P. A., Sylloge Fungorum omnium hucusque cognitorum. Vols. XIX and XX. *Index Iconum Fungorum* enumerans eorundem figuras omnes hucusque editas ab auctoribus sive antiquis sive recentioribus. Ductu et consilio P. A. SACCARDO. Congessit J. B. TRAVERSO. Roy. 8vo. Vol. XIX, pp. xi+1158; Vol. XX, pp. 1310. Sumptibus P. A. SACCARDO. Typis Seminarii. Patavii, 23 March 1910, and 25 May 1911.

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conducted in New York City.—J. R. DRUMMOND (Bot. Mag. *t. 8451.* 1912) describes and illustrates a new species of *Agave* (*A. disceptata*) supposed to be native of Central America.—A. A. HELLER (Muhlenbergia **8**:82–84. 1912) in continuation of studies on the genus *Lupinus* records a new species (*L. borealis*) from the Yukon region, Canada.—W. A. MURRILL (Mycologia **4**:163–169. *pl. 68.* 1912) under the title "Illustrations of fungi XI" describes and illustrates several species, 4 of which are new to science. The same author (*ibid.* 205–217) begins a series of articles on the "Agaricaceae of the Pacific Coast"; in the first article 12 new species are characterized.—C. R. ORTON (*ibid.* 194–204. *pls. 70, 71.* 1912) in a paper on "Correlation between certain species of *Puccinia* and *Uromyces*" describes a new fungus (*Puccinia uniporula*). The type was found on *Carex pubescens* Muhl., collected at London, Canada.—L. QUEHL (Monatsschr. für Kakteenk. **22**:102–105. 1912) describes and illustrates a new species of *Echinocactus* (*E. violaciflorus*) from Mexico.—C. REA and H. C. HAWLEY (Proc. Roy. Ir. Acad. **31**: part 13. pp. 1–26. *pl. 1.* 1912) in a report on the fungi of Clare Island, have published a new genus (*Candelspora*); the fungus was found on leaves of *Ilex aquifolia*.—A. REHDER (Rhodora **14**:97–102. 1912) records a new *Rhododendron* (*R. carolinianum*) from North Carolina and a hitherto undescribed form (*R. minus* f. *Harbisonii*) from Georgia.—L. W. RIDDLE (Mycologia **4**:125–140. 1912) enumerates 113 species of lichens, collected in Jamaica by the late Professor CLARA EATON CUMMINGS; the paper includes several new combinations and 11 species new to science.—S. SCHÖNLAND (Rec. Alb. Mus. **2**:251–253. *pl. 12.* 1912) describes and illustrates a new genus (*Neopatersonia*) of the Liliaceae from the region of Port Elizabeth, South Africa.—R. SCHLECHTER (Rep. Sp. Nov. **10**:480–486. 1912) has published 8 new species of orchids from Central America. The same author (Orchis **6**:63–69. *pls. 12, 13.* 1912) in an article entitled "Neue und seltene Garten-Orchideen" describes several novelties, including a new orchid (*Stelis Hennisiana*) native of Colombia.—O. E. SCHULZ (Bot. Jahrb. **46**:613–628. 1912) presents a revision of the genus *Clibadium*, recognizing 19 species, 3 being new to science.—F. J. SEAVER (Mycologia **4**:115–124. *pls. 66, 67.* 1912) publishes the results of a taxonomic study of the genus *Lasiosphaeria*, recognizing 10 species of which 2 are characterized as new.—E. E. SHERFF (Rhodora **14**:164. 1912) records a new variety of *Rudbeckia* (*R. subtomentosa* var. *Craigii*) from Missouri.—S. A. SKAN (Bot. Mag. *t. 8436.* 1912) describes and illustrates a new *Calceolaria* (*C. Forgetii*) from Peru.—M. SLOSSON (Bull. Torr. Bot. Club **39**:285–288. *pl. 23.* 1912) has published two new ferns from tropical America.—W. W. SMITH and G. H. CAVE (Rec. Bot. Surv. Ind. **4**:141–260. 1911) under the title "The vegetation of the Zemu and Llonakh valleys of Sikkim" enumerate somewhat over 1000 species of plants from the Selaginellaceae to the Compositae and include a new genus, namely *Parajaeschkea*, referred to the Gentianaceae.—W. W. SMITH (*ibid.* 273–282) in an article entitled "Some additions to the flora of Burma" describes several species new to science and proposes a new genus (*Craibiodendron*) of the Ericaceae.—A. T. SPEARE

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(Phytopathology **2**:135–137. *pl. 12.* 1912) describes and illustrates a new fungus (*Gibellula suffulta*), found on an unidentified species of spider at Wiamea, Hawaii.—P. C. STANDLEY (Proc. Biol. Soc. Wash. **25**:119, 120. 1912) proposes a new genus (*Wootonella*), based on *Ximenesia encelioides* var. *nana* Gray.—F. STEPHANI (Sp. Hep. **4**:801–824. 1912) has issued title-page and index to volume 4, and (*ibid* **5**:1–176) continues the record of species, many of which are new to science.—H. and P. SYDOW (Leafl. Philipp. Bot. **5**:1133–1147. 1912) have published 24 new species of fungi from the Island of Palawan, P.I., and include the following new genera: *Nematothecium* of the Perisporiaceae and *Discosiella*, a genus related to *Discosia*.—F. THEISSEN (Beih. Bot. Centralbl. **29**:45–73. 1912) under the title "Zur Revision der Gattung *Dimerosporium*" characterizes a new genus (*Dichothrix*) of the Eurotiaceae.—W. WEINGART (Monatsschr. für Kakteenk. **22**:83, 84. 1912) has described a new species of *Echinocereus* (*E. Weinbergii*) introduced into cultivation from North America, and (*ibid.* 106–109) a new species of *Cereus* (*C. Vaupelii*) from Haiti.—H. F. WERNHAM (Journ. Bot. **50**:156–164. 1912) presents a revision of the genus *Bertiera*, recognizing 33 species of which 5 are new to science.—K. M. WIEGAND (Rhodora **14**:117–161. *pls. 95, 96.* 1912) presents an interesting and thorough revision of the genus *Amelanchier* in eastern North America, recognizing 8 species of which 3 are characterized as new. The revision is of particular value on account of a clear key to the species and full citation of exsiccatae.—W. ZEH (Notizblatt **5**:268–273. 1912) has described several new species in the genus *Liagora* and includes one from California, one from Guadeloupe, and one from Brazil.—J. M. GREENMAN.

Periodicity of tropical vegetation.—On account of the abundance of its data, VOLKENS'[9] report on the results of his observations in Java, 1901–1902, is perhaps the most valuable of a series of recent articles upon the problems and conditions of foliar periodicity in the tropics. Exact records of the behavior of individual trees of over 100 species growing in the Buitenzorg Gardens show almost all possible variations of foliage conditions, from trees regularly deciduous once or twice a year, through evergreens with marked periodicity, to others with uniform foliage gradually renewed throughout the entire year. Attention is directed to the marked individuality not only of species and of individual trees of the same species, but also of individuals of different ages, and even of different branches of the same tree. VOLKENS shows that a moderate amount of climatic periodicity exists at Buitenzorg, especially in precipitation, relative humidity, and insolation; also that a large majority of the trees show a definite foliar periodicity, but concludes that no coincidence or causal connection can be established between the two classes of phenomena. He rejects as most improbable the influence of the salt content

[9] VOLKENS, G., Laubfall und Lauberneuerung in den Tropen. 8vo, pp. 142. Berlin: Gebrüder Borntraeger. 1912. *M* 3.80.

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of the soil water, and abandons the hypothesis that leaf-fall is due to an excess of stored food checking the activity of the leaf by preventing the removal of the products of photosynthesis. He finds the final cause of leaf-removal and leaf-renewal in the inherited, internal, unknown attributes of the protoplasm. He confesses that all his efforts to arrive at any explanation of these internal causes have been fruitless. External factors modify the action of these primary causes, but in a comparatively uniform climate like that of Java the modification is slight.

VOLKENS also reviews the work of WRIGHT[10] and others upon deciduous trees, and that of SMITH[11] which affords some data for certain evergreen species in Ceylon, and finds them in accord with his own observations.

In attempts to interrupt the regularity of leaf-fall, DINGLER[12] in Ceylon and KLEBS[13] in Java removed all the leaves from individuals of various species a few months before their regular time of shedding, and obtained a prompt renewal of the foliage and its persistence throughout the period in which they were usually leafless. DINGLER sees in this a proof of the efficiency of the inner cause in disregarding external conditions, while KLEBS, on the contrary, regards it as a response to external factors proving that a rest period is not required. Both these investigators have studied the behavior of deciduous European trees in the tropics, DINGLER[14] at a mountain station in Ceylon, and KLEBS at Tjibodas, Java, and found the usual European habit largely abandoned, new foliage and flowers being often produced twice in the year, while many species never became entirely leafless. Several resembled tropical species in having at one and the same time branches in full foliage, with bursting buds and in leafless condition, respectively. From these and many other experimental studies KLEBS reaches the general conclusion that periodicity of plant life is conditioned by periodicity of external factors.

In a more recent paper[15] KLEBS takes exception to VOLKENS' statement that tropical vegetation in Java is mainly periodic, claiming that when all the constituents of the forests about Buitenzorg and Tjibodas are considered, there

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[10] WRIGHT, H., Foliar periodicity of endemic and indigenous trees in Ceylon. Ann. Roy. Bot. Gard. Peradeniya **2**:415–516. 1905.

[11] SMITH, A. M., On the internal temperature of leaves in tropical insolation; also observations on the periodicity of the appearance of young colored leaves of trees growing in Peradeniya. Ann. Roy. Gard. Peradeniya **4**:229–298. 1909.

[12] DINGLER, H., Versuche über die Periodizität einiger Holzgewächse in den Tropen. Sitz. K. Bay. Akad. Wiss. München. pp. 127–143. 1911.

[13] KLEBS, G., Über die Rhythmik in der Entwicklung der Pflanzen. Sitz. Heidelberger Akad. Wiss. Abh. 23. 1911.

[14] DINGLER, H., Über Periodizität sommergünen Bäume Mitteleuropas in Gebirgsklima Ceylons. Sitz. K. Bay. Akad. Wiss. München. pp. 217–247. 1911.

[15] KLEBS, G., Über die periodischen Erscheinungen tropischer Pflanzen. Biol. Centralbl. **32**:257–285. 1912.

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is comparatively little periodicity. By a series of experimental cultures, carried on partly in Java and partly in the greenhouses at Heidelberg with tropical trees of periodic habit, he has succeeded, by varying the fertility of the soil, in obtaining varying responses from the same species and in greatly prolonging the period of continuous growth. This leads him to conclude that periodicity may be conditioned by the supply of food materials. He also calls attention to the fact that in attempts to relate periodicity to external factors only the more obvious climatic conditions have been considered, and that our data consist largely of comparatively crude observations. More exact studies upon an experimental basis are required. He concludes that the idea of a general primary rhythm in tropical plants, as advanced by SCHIMPER and now supported by VOLKENS and others, is contradicted by one series of facts, is rendered doubtful by other facts, and is supported only by such observations as up to the present time it has been impossible to subject to a searching physiological examination.—GEO. D. FULLER.

Paleobotanical notes.—WHERRY[16] has described three types of fossil wood from the Trias of Pennyslvania. The first, *Araucarioxylon virginianum* Knowlton, has been found previously in North Carolina, Virginia, and Connecticut. The second, *A. vanartsdaleni*, is separated as a new species on the lower medullary rays and predominance of uniserial pitting of the tracheids. The third is referred to the genus *Brachyoxylon* Hollick and Jeffrey, under the name of *B. pennsylvanicum*, because the pits, when uniserial, are usually scattered and circular, and when biseriate are either "distant and sub-opposite" or "alternate and hexagonal." This identification seems hardly justified, for the pits in *Brachyoxylon*, when double, are always alternate and closely compressed. Moreover, the most important diagnostic feature of that genus is the formation of traumatic resin canals. Without this reaction, WHERRY cannot properly refer his specimen to the genus *Brachyoxylon*.

In a second paper,[17] WHERRY discusses the evidence supporting the suggestion that the so-called "New Red" may represent deposits from the Lower Carboniferous to the Jurassic, and concludes that while there are no grounds for referring any of these beds to the Paleozoic, the absence of distinctive fossils except those of the Keuper type leaves it an open question whether there may not be also Bunter below and Jurassic above.—R. S. HOLDEN.

Earliest European angiosperms.—Dr. STOPES has described[18] three new genera from the lower Greensand of England, representing the earliest structurally known European angiosperms. The first, *Aptiana radiata*, has vessels

[16] WHERRY, EDGAR T., Silicified wood from the Triassic of Pennsylvania.

[17] ———, Age and correlation of the "New Red" or Newark Group of Pennsylvania.

[18] STOPES, MARIE C., Petrifactions of the earliest European angiosperms. Phil. Trans. Roy. Soc. London B **203**:75–100. *pls. 6–8.* 1912.

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with scalariform end walls, copiously pitted fiber tracheids, both uniseriate and multiseriate rays, and very few or possibly no wood parenchyma cells. The vessels and tracheids are of an undoubtedly primitive character, but the rays, according to recent investigations, represent a high state of development. The second, *Woburnia porosa*, has multiseriate rays, and parenchyma grouped around the vessels, as it is in such high families as the Leguminoseae, Ulmaceae, Oleaceae, etc. The third, *Sabulia Scottii*, is imperfectly preserved, but shows mainly uniseriate rays. Whether they represent the primitive condition, like certain species of *Alnus*, or are reduced, like *Castanea*, *Salix*, *Populus*, etc., it is impossible to say. Dr. STOPES seems to think that the antiquity of these specimens indicates that theirs is necessarily the primitive type of angiospermous wood structure. It is significant, however, that in formations considerably older than the Lower Greensand, there are abundant impressions of the Cupuliferae, which comparative anatomy has shown to represent the really primitive conditions.—R. S. HOLDEN.

A new cretaceous palm.—STEVENS[19] has described a new palm from the Upper Cretaceous of New Jersey, the fossil having been found on the beach at Seabright, not far from Sandy Hook. The details are well worked out and illustrated, and the name assigned is *Palmoxylon anchorus*. It seems that petrified stems of palms are not so rare as has been supposed, and the author thinks it probable that palms occur abundantly from the Upper Cretaceous on, both on the coastal plain and in the formations of the continental interior.—J. M. C.

Haustorium of Striga.—Miss STEPHENS[20] has investigated the remarkable haustorium of *Striga lutea*, a South African annual growing as a root parasite on native grasses and on maize. The haustoria arise exogenously from the many adventitious roots, and when one encounters a root of the maize it bores its way into the host by means of a ferment, a line of tracheids is formed down the center of the haustorium, and vascular connections are established with the host.—J. M. C.

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[19] STEVENS, N. E., A palm from the Upper Cretaceous of New Jersey. Amer. Jour. Sci. **34**:421–436. *figs. 24.* 1912.

[20] STEPHENS, EDITH L., The structure and development of the haustorium of *Striga lutea*. Ann. Botany **26**:1067–1076. *pl. 93.* 1912.

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THE

BOTANICAL GAZETTE

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TOXICITY OF SMOKE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 171

LEE I. KNIGHT AND WM. CROCKER

I. Introduction

(WITH FOUR FIGURES)

Extensive unpublished experiments have been conducted in this laboratory to determine the reliability of the etiolated epicotyl of the sweet pea as a test for the presence of traces of heavy hydrocarbons in the atmosphere. As an outgrowth of this work, we have had occasion to study the response of this organ to smoke produced by the burning of various carbon-bearing substances, with the idea of discovering the constituent or constituents that produce the response.

The complete statement of the response of this seedling to gaseous impurities will involve two additional papers, one under the title "Is methane toxic?" and the other "The sweet pea epicotyl as a delicate test for heavy hydrocarbons." Both of these papers will be published shortly.

NELJUBOW (**25**) has shown that the etiolated epicotyl of the pea seedling has an abnormal growth in "laboratory" or "impure" air. We may speak of the abnormality as a triple response: change of negative geotropism to diageotropism, increased growth in thickness, and reduced rate of growth in length. We tested about 20 varieties each of garden peas and sweet peas, and found the sweet peas in

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general considerably the more sensitive. Two varieties of these, under the trade names Earl Cromer and Gladys Unwin (Vaughan's Seed Store), were especially sensitive.

II. Methods

GROWING THE SEEDLINGS

Gladys Unwin and Earl Cromer are both hard-coated varieties. After 24 hours' soaking in water, about 10 per cent swell, and 10 days are required for all to swell. Consequently, in order to get uniform growth in the seedlings, the coats are scratched with a file and the seeds soaked for 15 hours in distilled water. They are then thoroughly shaken up with several changes of distilled water and placed in a thin layer between sterile wet filter papers and allowed to germinate. When the longest hypocotyls have reached a length of 5 mm., the seeds are transferred to wet sterile absorbent cotton in large petri dishes and allowed to grow in total darkness at 20°–24° C. until the epicotyls have an average height of 2–3 cm. This method gives cultures fungus-free and of far more nearly uniform growth than can be obtained by less careful methods. It also gives cultures bearing only the more vigorous seedlings. This is especially important, for sensitiveness to atmospheric impurities rises with the vigor of the seedlings. With all these precautions there is considerable irregularity in the rate of growth of the various epicotyls in a culture. The entire process must be carried on in what the German workers have called pure air, which means air practically free from the heavy hydrocarbons, especially ethylene. A quantity of this substance equaling one part in ten million of atmosphere interferes with the growth of the seedling.

In case the gas to be tested is very soluble in water, it is necessary to protect it against contact with the moist cotton bearing the roots. This is done by covering the substratum with low-melting paraffin mixed with pure paraffin oil. In many cases it was also found desirable to have a desiccating agent in the experimental chamber to keep its walls free from water given off by transpiration. This especially holds for gases like SO_2 and NH_3.

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METHOD OF EXPOSING TO GASES AND VAPORS[1]

The exposure to gas or vapor was made in galvanized iron cans of the type shown in fig. 1, and of three capacities, 10, 50, and 100 liters. Each can consists of two pieces, the can proper and the bottom. The can proper has at *a* a side tube bearing a no. 3 two-holed rubber stopper. The stopper is equipped with glass tubes, rubber tubes, and screw clamps. The lower edge of the can has an out-turned brim, 1 cm. wide, at right angles to the sides of the can; this gives the can close continuous contact with the bottom. The bottom is a galvanized iron disk with 3 mm. of the edge turned up at right angles to the plane of the disk. The brim of the can fits closely inside the upturned margin of the bottom. To seal a culture in the can, it is placed on the bottom piece, the can set in position, and the gutter above the brim of the can carefully sealed with molding clay mixed with vaseline in such proportions as to give the desirable consistency. The seal will hold against a very considerable unequal pressure of gas. Vaseline was chosen as the mixing medium because it does not give off any fumes injurious to the seedlings and makes a material that maintains the same consistency after years of use. If the gas studied required the use of only a few cc., it was forced in through one of the tubes at *a* under a small head of mercury or water. Mercury was used in case the gas was very soluble in water, otherwise water was used. If a larger volume of the gas was required, suction was applied to one of the tubes at *a*,

FIG. 1.—Apparatus for exposure to gases and vapors: explained in text.

[1] The description of methods here will cover the whole field of work, thereby avoiding redescription in later papers. For that reason many matters mentioned here do not apply to the work on smoke.

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after which it was clamped. This suction served as the force for drawing in the gas through the second tube.

In cases where very large quantities of the gas were required, as with methane, the can was replaced by a bell jar and a water seal used. The whole apparatus was then placed in a dark chamber. To make sure of the reliability of the can, this method was also frequently used as a check in case of gases demanding only low concentration and not readily absorbed by water. If the vapor of a very volatile liquid, like ethyl ether, was to be used, a measured quantity of it was forced from a pipette into the upturned end of one of the glass tubes at *a*. A glass dish bearing absorbent cotton was attached just under the inner down-turned end of the glass tube. The liquid volatilized from the cotton and its vapor was distributed throughout the can. Applying the gases and vapors in this way, at the most distant point from the seedlings, insured that they would not at any time receive higher than the finally distributed concentration. In case the vapor of a slightly volatile liquid, like propyl alcohol, was to be applied, the desired amount was dropped on absorbent cotton and quickly sealed in the can with the cultures. In this case, of course, the clamps at *a* are screwed down or the hole provided with a solid cork.

The cultures are always subjected to the influence of the gas for three days, the same period used in our experiments with the carnation. At the close of an experiment the epicotyls in any culture of controls vary in height from 5 to 13 cm., while the cultures subjected to injurious concentrations of gases show less growth.

In this method of experimentation, as is seen, the epicotyls are not subjected to the same concentration during the entire three days, for the gas is applied only at the beginning of the experiment. The concentration must fall to a degree varying with the different gases, due to absorption by the plant and substratum, and to some extent due to a slow diffusion outward through the seal. If the gas is one that is readily absorbed by the plant, as SO_2, the method probably more nearly determines the lethal dose. In the case of the carbon-bearing gases (acetylene, ethylene, propylene, methane, and carbon monoxide), with the exception of acetylene, which is

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rather soluble in water, the method certainly gives a very close approximation to the constant concentration necessary to give a response. The object of the work was to determine the nature of the response given by the several gases and vapors and to approximate the concentration necessary to produce it. For this purpose the method is adequate.

III. Historical

1. RESPONSE OF THE PEA EPICOTYL

a) *Horizontal nutation*

As has been stated, the epicotyl of the pea seedling grows prostrate or horizontal in "laboratory" air. NELJUBOW (**25**) has spoken of this response as a *horizontal nutation*, and mentions ethylene and acetylene, both constituents of illuminating gas, as especially effective in producing it. He has shown (**26**), also, that the response is not limited to the pea epicotyl, but appears in the etiolated epicotyls of *Ervum lens*, *Lathyrus odoratus*, *Vicia sativa*, and *Tropaeolum*. SINGER (**42**) has observed the same for the potato stem. NELJUBOW has shown that the response in the pea epicotyl in an atmosphere containing ethylene varies with the concentration of ethylene. Beginning with the higher concentrations and passing to the lower, he mentions the following grades of response: (1) no growth, death; (2) no elongation, a swollen knob; (3) elongation slow, swelling, diageotropism; (4) elongation faster, little swelling, diageotropism; (5) like (4) except obliquely placed; (6) erect, but growth reduced by half.

The horizontal nutation has been a subject of no little investigation. With mere mention we can pass over WIESNER'S (**43**) conception of undulating nutation induced by darkness, and RIMMER'S (**39**) autonomic nutation induced by dryness, for at that time there were not sufficient data available for a rational interpretation of the response. MOLISCH (**20**) and KÖRNICKE (**17**) concluded that impurities of laboratory air affect geotropic and heliotropic sensibility in opposite ways, weakening the former and strengthening the latter. MOLISCH (**21**, pp. 170, 171) has apparently abandoned the idea of increased heliotropic sensibility.

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RICHTER (32, 33, 34) speaks of the impurities weakening negative geotropism and has continuously maintained that they increase heliotropic sensibility. GUTTENBURG (13) has spoken of the horizontal nutation as due to weakened negative geotropism and vigorously denied increased heliotropic sensibility. He attributes the conclusion of other workers on the latter point to inaccuracies in experimentation, especially the failure to use the clinostat, thereby eliminating the antagonistic action of gravity.

NELJUBOW (26) has maintained since 1901 that the response is induced diageotropism. The evidence set forth in his last paper seems conclusive, marked as it is by excellence of experimentation. He criticizes the other workers for using "laboratory" air in which the quantity of effective impurity must vary from hour to hour, and in which the amount of impurity cannot be measured at any time. He used mixtures of pure air with 1–3 ppm. of ethylene. To maintain constant concentration the mixture was renewed daily. In this atmosphere on a horizontal clinostat the etiolated pea epicotyls showed great reduction in rate of elongation, also swelling but not bending. When grown in the same atmosphere off the clinostat, they showed the same characters with the addition of horizontal nutation. If in such an atmosphere the epicotyls were raised or lowered out of the horizontal position, they again assumed it. NELJUBOW maintains that diageotropism is the only assumption that can explain this behavior. He emphasizes that there is no autonomic nutation determining the direction in which the epicotyl turns to assume the horizontal position, but that it is entirely determined by its position in relation to the pull of gravity. RICHTER (34), working with seedlings of *Vicia sativa*, *V. villosa*, and *Pisum sativum*, shows that such a statement can hold only for epicotyls more than 1 cm. tall. On a clinostat or in "impure" air which "weakens" negative geotropism, the young etiolated epicotyls turn "backward" (in the direction in which the closed side of the curved tip faces) and crowd themselves closely against the substratum. This is an autonomic nutation incapable of manifesting itself off the clinostat in pure air on account of the counteraction of negative geotropism. Judging from the work of both NELJUBOW and RICHTER, the horizontal nutation of the etiolated

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epicotyl of the pea, if less than 1 cm. tall, is due to the joint action of autonomic nutation and diageotropism; but, if taller than 1 cm., it is due to diageotropism alone. It should be mentioned in this connection that NELJUBOW worked mainly with taller epicotyls, which probably accounts for the autonomic nutations escaping detection by his careful methods.

b) The swelling

The increased diameter or swelling of a plant organ in the presence of poisons is apparently a rather commonly observed phenomenon. COOK and TAUBENHAUS (5) observed that in proper concentration of tannin the mycelia of various fungi tend to become short, thick, and much septate. GROTTIAN (12) finds that anaesthetics, especially chloroform, produce a swelling in the root just back of the tip, with constrictions above and below. NĚMEC (27) finds that chloral, ether, benzine, benzene, and alcohol vapors have a similar effect.

The anatomical structures of the swollen zone, along with the physiological condition causing the peculiar structure, has been a subject of some comment. As RICHTER (35) has stated, the swollen region shows an abundant development of collenchyma, also numerous rifts more or less lined with cork. RICHTER (36) has related the swollen condition and the development of rifts to excessive osmotic pressure induced by the poisons. So far as his cited articles are concerned, there is no evidence that he has made any measurements of osmotic pressures. His conclusions are based on two lines of indirect evidence. First, many observers have found an increase in osmotically active substances in plants grown in an atmosphere bearing poisons. JOHANNSEN has shown that soluble sugars increase in plants in the presence of ether and other anaesthetics. PRIANISCHNIKOW (29) has shown that etiolated lupine seedlings grown in laboratory air have a much greater amount of asparagin than those grown in pure air. The following table (p. 344) gives the difference, in percentage, wet weight, of asparagin in 12-day seedlings in pure air and laboratory air.

GRAFE (10) has shown that soluble sugars accumulate in plant organs at the expense of starch in an atmosphere bearing formalde-

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hyde. GRAFE and RICHTER (11) have lately demonstrated that an atmosphere bearing acetylene or carbon monoxide changes radically the course of metabolism in various plant organs. In seedlings of *Vicia villosa* and *V. sativa* and stems and tubers of the potato, carbon monoxide (0.038 to 0.29 volume per cent in air) causes an increase in the sugar and amino content. In fatty seeds (squash and mustard) there is a decrease in sugar and amino compounds and an increase in glycerine and fatty acids. Acetylene interferes with the synthesis of sugar from glycerine and condensation of glycerine and fatty acids to fats.

PURE AIR		LABORATORY AIR	
Cotyledon	Epicotyl	Cotyledon	Epicotyl
0.140	0.289	0.348	0.625

The second evidence that RICHTER offers for poisons causing increased osmotic pressures is the fact that they often produce proliferation of sublenticular tissue similar to the substomatal proliferations or intumescences caused by high humidity. Very often, also, the lenticular protrusions, as well as other tissues, show guttation in the presence of poisons, which RICHTER interprets as indicating high osmotic pressure. Measurements of osmotic pressure would certainly be more to the point in the case of pea seedlings, though they might give less ground for philosophy and even a reverse conclusion. Aside from known relations to osmotic pressure, and only indirectly bearing on the point under discussion, it is well known that poisons, especially atmospheric impurities, produce considerable alteration in the structure and form of plants. The late work of GATIN (**8, 9**) on the effect of tarred roads on vegetation furnishes excellent examples of this. He finds that the fumes of tar bring about the disappearance of endodermis, alteration in the size and number of layers of cells in the cortex and other regions of the stem, and the transformation of doubly compound leaves into singly compound ones. Of less fundamental importance, perhaps, is the disappearance of starch and the formation of cork on leaf organs and young stems. RICHTER (**37**) has lately

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summarized the effects of poisons upon the development of plant structures. Under modifications due to increased cell pressure, he mentions inhibition of growth in length, favoring of growth in diameter, splitting of the tissues with formation of rifts, lenticular and intumescence formation, and maceration in the living body. Other modifications that he relates to the rise of turgor are collenchyma formation, thickening of the epidermis, vacuolization of the nucleus, and fusion of the nuclei.

These two lines of general evidence are very interesting in connection with the response of the pea seedling, but after all they leave essentially untouched the real solution of the physiology of the response. This becomes more evident when it is remembered that our work shows three distinct types of response of this seedling to atmospheric impurities: (1) that produced by ethylene, acetylene, propylene, illuminating gas, various sorts of smoke, and possibly methane, and characterized by decreased rate of elongation, swelling, and diageotropism; (2) that produced by ether, chloroform, benzol, toluol, thiophene, xylol, cumene, and other substances, and characterized by decreased rate of elongation and swelling but not diageotropism; (3) that produced by ethyl alcohol, propyl alcohol, pyridine, hydrogen sulphide, hydrogen chloride, and other substances, and characterized by decreased rate of elongation, but neither swelling nor diageotropism. A careful detailed study of osmotic pressure, permeability, and metabolic (enzymatic, acid, respiratory, etc.) behavior of the seedlings, in each group of poisons might throw much light on the internal intimate physiology of the three types of response. A detailed study in this line might also relate diageotropism more closely with physical and chemical characters of the organ. This organ furnishes especially desirable material for such a study because of the ease with which it is changed from a negative to a diageotropic organ.

2. EFFECT OF TOBACCO SMOKE

MOLISCH has shown that tobacco smoke is extremely toxic to many plants. In his first paper (**22**) he reports the effect of tobacco smoke on various seedlings and microorganisms, and in a second paper (**23**) the effect upon adult plants. A third paper (**24**)

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brings together all the main conclusions of the work, and emphasizes the bearing of the findings upon the growth of plants in dwellings, laboratories, etc.

Seedlings (*Vicia sativa*, *Pisum sativum*, *Cucurbita Pepo*, *Phaseolus vulgaris*, and others) are very sensitive to tobacco smoke. In its presence *Vicia sativa* epicotyls show what we have termed the triple response, also they fail to develop anthocyanin, a feature RICHTER (**38**) has observed for many plants grown in laboratory air. MOLISCH states that one to three whiffs of cigar or cigarette smoke in a 4.3-liter container caused the triple response. Smoke of paper, straw, and wood has effects similar to tobacco smoke, while fumes of nicotine have little influence on the seedlings. Carbon monoxide, pyridine, and hydrogen sulphide, in considerable dilution in the atmosphere, produce effects similar to smoke. MOLISCH quotes PONTAG as showing that cigar and cigarette smoke bear considerable quantities of carbon monoxide. On the basis of these data, MOLISCH concludes that carbon monoxide is probably the constituent determining the toxic limit of tobacco smoke for seedlings. Acquaintance with the work of NELJUBOW (**25**), CROCKER and KNIGHT (**6**), and LEHMANN (**18**) should have led him to recognize the high toxicity of ethylene for epicotyls of seedlings and other plant organs, the rather low toxicity of carbon monoxide, and the universal presence of ethylene in tobacco smoke. This immediately suggests the probability of ethylene being the constituent determining the toxicity for seedlings. MOLISCH's "whiff" methods are poorly adapted for matching the amount of carbon monoxide in the applied smoke against the amount demanded to produce the response.

Many microorganisms are likewise remarkably sensitive to tobacco smoke. A whiff of tobacco smoke blown across a culture of *Pseudomonas lucifera* "puts it out" in 0.5–1 minute. It readily recovers its power to phosphoresce when returned to sea water. *Chromatium vinosum*, *Beggiatoa*, *Spirillum* sp., *Amoeba*, *Vorticella*, *Paramoecium*, *Didymium nigripes*, and *Gymnodimium fucorum* are very sensitive to tobacco smoke, while *Pinnularia* and *Phycomyces nitens* are rather resistant.

Adult vascular plants behave variously toward the impurity.

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Tradescantia guianensis, *Selaginella Martensii*, *Tolmiaea Menziesii*, *Eupatorium adenophorum*, and various echeverias are not interfered with at all by low concentrations of smoke in the air, and only slightly inhibited in their growth by great concentrations. The mature plants that are sensitive to tobacco smoke manifest it in three ways: (1) by chemotactic movements of the leaves; the leaves of *Boehmeria utilis* and *Splitgerbera biloba* showed epinastic movements when in a glass chamber of 4.5–7 liters with 1–3 whiffs of cigar or cigarette smoke; in *Boehmeria* the movement continues beyond the vertical position, with the formation of spirals in the petiole; (2) by lenticular protuberances; the development of lenticular protuberances occurred in sprouts of the potato and stems of *Boehmeria polystachya* and *Goldfussia glomerata* in the presence of tobacco smoke; while in *Salix rubra* and *Sambucus nigra* such protuberances develop in moist air, the process is greatly hastened by tobacco smoke; guttation commonly occurs in this lenticular tissue, due, as MOLISCH assumes, to high osmotic pressure; (3) by fall of leaves; tobacco smoke causes leaf fall in many plants; this is especially true of leguminous forms; 24–48 hours of exposure to tobacco smoke causes almost complete loss of leaves in *Mimosa pudica*, *Caragana arborescens*, *Robinia pseudacacia*, *Halimodendron argenteum*, and others; paper and wood smoke were likewise very effective in producing leaf fall, and nicotine very weakly so. MOLISCH states that in the mature plants he was not able to determine the constituent of tobacco smoke that does the injury.

IV. Observation and experimentation

AN OBSERVATION

A mishap in the greenhouses of this laboratory has some of the virtues of a real experiment. An attempt to kill the insects by the common method of burning tobacco stems resulted in the acute poisoning of many of the plants. This application of a high concentration of smoke for a short time did not, of course, show responses in the nature of nasties, swellings, abscissions, and nulled tropisms, as observed by MOLISCH with the application of lower concentrations

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for long periods. The injury in this case must be stated in terms of the region and extent of killing. The records were taken five days after the mishap.

The following showed no injury: BRYOPHYTES, *Marchantia polymorpha*, *Conocephalus conicus* (not under spray); PTERIDOPHYTES, *Cyrtomium falcatum*, *Azolla caroliniana*, *Salvinia natans;* SPERMATOPHYTES, cycads, when not actively growing (*Dioon edule*, *D. spinulosum*, *Zamia floridana*, *Macrozamia Miquelii*, *Encephalartos cycadifolia*, *E. Lehmanii*, *E. Altensteinii*, *E. horridus*, *E. caffer*, and *Ceratozamia mexicana*), *Hibiscus rosa-sinensis*, *Zebrina pendula*, *Begonia semperflorus* (flowers and foliage), *Pelargonium zonale*, *Ficus elastica*, *F. lyria*, *Sagittaria variabilis*, and *Lemna trisulca*.

The following forms showed evident injury: BRYOPHYTES, *Riccia* (in pots on benches, all killed), *Conocephalus conicus* (growing under spray, all killed); PTERIDOPHYTES, *Lygodium* sp. (leaves all killed at tips and margins and many halfway back), *Pteris longifolia cristata* (tips and margins of leaves killed, brown spots on leaves), *Nephrolepis bostoniensis* (slight injury), *Aspidium longifolium* and *A. nidus* (some of the plants killed to the ground), *Alsophila denticulata* (badly injured); SPERMATOPHYTES, *Impatiens Balsamina* (all the older leaves brown-spotted), tomato (leaves entirely killed in most cases, but only at the tip in some), *Persia gratissima* (older leaves all killed), *Stevia serrulata* (all but youngest leaves killed), *Vinca alba* (ends and margins of leaves slightly injured), *Coleus* spp. (all older leaves fallen, young plants showed less injury). It is of interest that *Conocephalus conicus* growing on the benches was not injured at all, while a vigorous culture that had been growing for a long period under a spray was completely killed. It is possible that good water supply caused the development of a loose, poorly protected structure. It is likewise possible that the great surface of the spray water kept it nearly saturated with the poison of the smoke. From the data given above, one can see that in general the better cutinized forms are more resistant. Some will be interested in comparing these injuries with those from illuminating gas observed in a greenhouse by WILCOX (**44**). There is evidence to indicate that both injuries are due to a common substance, as we will see later. In the case reported by WILCOX, the poisoning

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was more acute, due to longer application and possibly to greater concentration of the toxic material.

EXPERIMENTS

We will publish only a type experiment under each head, but in every case the experiment has been repeated several times to make sure the type experiment tells the truth. As has already been stated, we used the etiolated epicotyl of the sweet pea as the plant organ for testing the toxicity of smoke and its constituents, for we learned from our earlier experiments its behavior toward a great number of gaseous impurities, including the main constituents of smoke. This renders the determination of the constituents fixing the toxicity of smoke a simpler matter. Since the responses of the seedling to certain smokes and the variation of response with concentration is similar to the behavior toward ethylene, it is well to have in mind NELJUBOW'S (**26**) statement of the six types of response, varying with the concentration of the ethylene. They will furnish the data for an interpretation of the experimental results given below. Beginning with the higher concentrations, the responses are: (1) no elongation, death; (2) no elongation, vertical position, a knoblike swelling; (3) considerable elongation, swelling, horizontal position of the growing swollen part; (4) elongation greater, little swelling, horizontal position of part grown in ethylene-containing atmosphere; (5) like (4) except obliquely placed; (6) erect, but elongation rate reduced by half. Our failure to get a strictly horizontal position in many cases where NELJUBOW obtained it may be due to the fact that he changed the gas every day, thus maintaining an essentially constant concentration, while we applied the gas once and allowed it to stand for three days. The gradual absorption of the gas by plant, substratum, etc., may dilute it so that the epicotyl partly recovers its upright position. For our purpose, however, one application of the gas is adequate.

Experiment I.—Effect of unwashed smoke

When the experiment was set up, the etiolated epicotyls (Gladys Unwin) were 2–3 cm. tall, slim and vertical. The duration of exposure was three days. The following data show the sorts and

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concentrations of the smokes used, along with condition of the epicotyls at the close of the experiment:

1. Check (in duplicate) in 10-liter chamber; epicotyls 6–11 cm. tall, vertical and slim.

2. Lighted cigarette sealed in 10-liter chamber; epicotyls 2.5–3.5 cm. long; swelling 0.5–1 cm. long; shorter swelling vertical and longer ones declined as much as 90°.

3. Lighted pine splinter in 50-liter chamber; epicotyls 3–5 cm. long; swelling 1–2 cm.; declination 50°–90°.

4. Lighted piece of linen paper (not giving lignin test) in 10-liter chamber; epicotyls 3–3.5 cm. long; swelling knoblike; no declination.

5. A lighted sheet of ashless filter paper (6 cm. diameter) in 10-liter chamber; epicotyls 1–2 cm. long; swelling 1–2 cm.; declination 60°–90°.

6. Two lighted straws (12 cm. long) partly burned in 10-liter chamber; epicotyls 3–3.5 cm. long; swelling knoblike, to 1 cm. long; declination 0°–90°.

7. Three whiffs of cigarette smoke in 10-liter chamber; reaction almost identical with 6.

8. 0.13-gm. linen paper burned as open sheet in 10-liter chamber; epicotyls 3–5 cm. long; swelling 1.5–2.5 cm.; declination 60°–90°.

9. 0.06-gm. linen paper burned in 10-liter chamber; epicotyls 4–7 cm. long; no swelling; diameter everywhere greater than in checks; declination 0°–15°.

10. 0.09-gm. linen paper burned in 10-liter chamber; reaction about the same as 9.

11. 1.45-gm. linen paper burned in 100-liter chamber; epicotyls 2.5–3.5 cm. long; swelling 0.5–0.75 cm.; slight declination.

12. 1.45-gm. linen paper burned in 50-liter chamber; reaction about as 11.

13. 0.36-gm. linen paper in 100-liter chamber; epicotyls 4–6.5 cm. long; no swelling, but larger diameter than checks; declination 20°–40°.

From this experiment it is evident that the smoke from the cellulose and lignin compounds is rather toxic. In agreement with MOLISCH, it shows that the toxic effect of tobacco smoke is not due to substances peculiar to tobacco, but is as marked for the smoke of pure cellulose. The unwashed smoke from 0.13 gm. of cellulose in 10 liters gives a response lying between NELJUBOW'S responses 3 and 4.

Experiment II.—Effect of washed smoke

In preparing the smoke, the cigar or cigarette (tobacco or paper) was smoked by suction and the smoke washed through two special wash bottles, one containing 15 per cent H_2SO_4, the other 40 per cent NaOH. According to LEHMANN (18), the first removes all

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NH_3, nicotine, tar, and solids, while of course the latter removes CO_2 and H_2S. There results a mixture of colorless gases which is stored over water. This method of storage is adequate, since the most toxic constituent of the smoke is very slightly soluble in water, as shown by the slight fall in toxicity when thus stored, also by evidence given later in the paper.

To obtain the cigarette smoke used in the following experiments, 7 Murad cigarettes, weighing 1.3 gm. each, were two-thirds consumed, with a yield of 10 liters of gas. Each liter of smoke, therefore, results from the smoking of 0.6 gm. of cigarette; 20 liters of cigar smoke were produced by 15 gm. of cigars; each liter of smoke required 0.75 gm. of cigar. The paper smoke was derived from a cigarette of bond paper not giving lignin tests; 4 liters of smoke were produced from 1.4 gm. of paper; each liter was derived from 0.35 gm. of paper. So far as we know, the tobacco and paper smoke thus washed will contain, in common, nitrogen of the air drawn through in smoking, more or less unused oxygen, certain dry distillation gases of the carbon compounds involved (methane, ethylene, acetylene, and carbon monoxide), and perhaps higher homologues of methane, ethylene, and acetylene. The tobacco smoke will contain in addition traces of pyridine and perhaps other compounds. In this experiment the epicotyls in each culture at the beginning of the exposure varied from 2 to 3 cm. in height. The seedlings were subjected to the smoke for three days in total darkness at 20° to 24° C. The following data give the various concentrations and varieties of smoke used, along with the condition of the epicotyls at the close of the experiment.

1. Check culture in 50-liter chamber; epicotyls 6–12 cm. tall, vertical and very slim.

2.[2] 25 cc. of cigar smoke (output of 0.0188 gm. of cigar) in 50-liter chamber; epicotyls 4–7 cm. tall; greatest declination 30°; no swelling; greater diameter than check.

3. 50 cc. cigar smoke (output of 0.0375 gm. of cigar) in 50-liter chamber; epicotyls 3.5–4.5 cm. long; swollen; declined portion 1.5–2.5 long, with a declination of 75°–90°.

[2] In all the work the smoke was measured under existing atmospheric pressure. No corrections for barometric pressure and temperature were deemed necessary, for a doubling of the concentration was required to give noticeable differences in response, hence the errors of this method were far beyond detection by the seedling.

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4. 100 cc. cigar smoke (output of 0.075 gm. of cigar) in 50-liter chamber; epicotyls 3.5–4 cm. long, with swollen regions 0.75–1.5 cm. long; swollen zones varying from upright to horizontal; the shorter swollen upright zones indicate that there is no growth in length.

5. 130 cc. cigar smoke (output of 0.097 gm. of cigar) in 50-liter chamber; many epicotyls showed knoblike swellings; no growth in length and no declination; many others were dead.

6. 200 cc. cigar smoke (output of 0.15 gm. of cigar) in 50-liter chamber; epicotyls mostly dead; living ones vertical, with a knoblike swelling; no growth in length.

7. 330 cc. of cigar smoke (output of 0.25 gm. of cigar) in 100-liter chamber; condition of epicotyls between that of 5 and 6.

8. 40 cc. of cigarette smoke (output of 0.024 gm. of cigarette) in 10-liter chamber; epicotyls 3–4.5 cm. long; swollen zone 1–2 cm. long; declination of swollen portion 80°–90°.

9. 20 cc. of cigarette smoke (output of 0.012 gm. of cigarette) in 10-liter chamber; epicotyls 3–6 cm. long; swollen portion 2–3 cm. long; declination of swollen part 70°–90°.

10. 10 cc. cigarette smoke (output of 0.006 gm. of cigarette) in 10-liter chamber; epicotyls 4–9 cm. long; little declination; no swelling; diameter of epicotyls greater than that of checks.

11. 20 cc. paper smoke (output of 0.007 gm. of paper) in 10-liter chamber; epicotyls 3–4.5 cm. long; swelling 0.75–1.5 cm. long; swollen portion vertical to horizontal.

12. 10 cc. paper smoke (output of 0.0035 gm. of paper) in 10-liter chamber; epicotyls 4–5 cm. long; swelling 1–2.5 cm. long and declined 70°–90°.

Several things are evident from these experiments. The smoke of paper and tobacco cigarettes is still very toxic after thorough washing with 15 per cent H_2SO_4 and 40 per cent NaOH. Later data will show that the constituents thus washed out have a comparatively low magnitude of toxicity. It becomes probable then that the high toxicity of paper and tobacco smoke is determined by the dry distillation carbon-bearing gases. Figuring on the basis of 10-liter containers, 10 cc. of cigar smoke (output of 0.0075 gm.), 40 cc. of cigarette smoke (output of 0.024 gm.), and 10 cc. paper cigarette smoke (output of 0.0035 gm.) give the third response mentioned by NELJUBOW (reduced rate of elongation, swelling, and horizontal position of the swollen part).

On the basis of the amount of washed smoke necessary to give the response, the cigar and paper cigarette smokes are about equally effective, and the tobacco cigarette smoke about one-fourth as

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effective; while on the basis of the dry weight necessary to produce the smoke, the paper is more than twice and the cigarette only about one-third as effective as the cigar. The toxicity of the several smokes undoubtedly depends in part on the oxygen supply during the smoking. This will determine to some degree the amount of dry distillation gases escaping oxidation, although much of these will escape oxidation under any condition, for the heat is sufficient beyond the ignited portion of the cigar or cigarette to cause dry distillation, and here no burning of the dry distillation gases can occur. When the same paper used in making the paper cigarettes was burned as an open sheet in the 10-liter container, it required 0.14–0.21 gm. to give NELJUBOW's third response. When burned in this way, the paper smoke is approximately 0.02 as toxic for this seedling. Burning the open sheet insures a more complete oxidation of the dry distillation carbon-bearing gases, both because of better oxygen supply and because of surer contact with the flame. It should be stated that the paper cigarettes used, though rolled only to moderate tightness, were difficult to smoke in the machine. They required considerable more suction than the cigarette and probably had low oxygen supply, as later analyses will indicate.

Experiment III.—Effect of washed smoke and chemical analyses

Two paper cigarettes, one loosely rolled and the other tightly, were smoked and washed with 15 per cent H_2SO_4 and 40 per cent NaOH and stored separately. The analyses of this sort of smoke according to the methods described by HEMPEL (14) are as follows:

Loosely wrapped paper cigarette; 4.78 gm. of paper smoked, with a yield of 8384 cc. of washed smoke.

	A	B
Volume of smoke taken for analysis	99.6 cc.	99.9 cc.
Volume after absorption with 40 per cent NaOH	99.6	99.9
Volume after absorption with bromine	99.5	99.9
Volume after absorption with phosphorus	99.5	99.9
Volume after absorption with ammoniacal cuprous chloride	84.4	85.0
Volume of CO	15.1	14.9

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This analysis gives a trace of heavy hydrocarbons (bromine-absorbed gases) and approximately 15 per cent of carbon monoxide. The figures show that each gram of paper produced 263 cc. of CO. This yield is very high when compared with the yield from tobacco in cigarettes, cigars, and pipe as reported by LEHMANN (18). In these it varies from 15 to 101 cc. of CO per gram of tobacco. Our figures may be a little high, due to incomplete drying of the stub before weighing.

Tightly wrapped paper cigarette. In this case 3.41 gm. of paper produced 7357 cc. of washed smoke.

Analysis	A	B
Volume of smoke taken for analysis	97.6 cc.	92.4 cc.
Volume after absorption with 40 per cent NaOH	95.8	90.6
Volume after absorption with phosphorus	95.8	90.6
Volume after absorption with bromine water	95.8	90.6
Volume after absorption with ammoniacal cuprous chloride	81.1	77.0
Volume of CO	14.7	13.6

In this analysis considerable CO_2 appears. On the basis of the CO_2-free smoke the CO constitutes 15+ per cent, approximately the same percentage shown in the analysis of the loosely rolled cigarette. There is not a measurable amount of heavy hydrocarbons, but in an analysis like this, where no corrections are made for temperature changes, it is possible to leave undetected 0.2 cc. In this case each gram of paper produced 327 cc. of CO, an even higher yield than given by the loosely rolled cigarette. This too is probably a little high, due to insufficient drying before weighing the stub back.

Effect on the seedlings.—At the beginning of the experiment the epicotyls were 2–3 cm. tall. The cultures were sealed in 10-liter cans and subjected to the smoke for 3 days. The following data show the nature and concentration of the smoke used, along with the condition of the seedlings at the close of the experiment.

1. Check; epicotyls 5–13 cm. tall, vertical and slim.

Washed smoke from loosely rolled paper cigarette

2. 10 cc.; epicotyls 3.5–5 cm. long; swollen portion 1–2 cm. long, with declination of 75°–90°.

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3. 20 cc.; epicotyls 3–4.5 cm. long; swollen portion 1–1.5 cm. long, with declination of 75°–90°.

4. 50 cc.; epicotyls 3–4 cm. long; swollen portion 0.5–0.75 cm. long, with little or no declination.

Washed smoke from tightly rolled paper cigarette

5. 10 cc.; epicotyls 3–4.5 cm. long; swollen portion 1–1.5 cm. long, with declination of 70°–90°.

6. 20 cc.; epicotyls 3–4.5 cm. long; swollen portion 0.75–1.5 cm. long, with declination of 75°–90°.

7. 50 cc.; epicotyls 3–4 cm. long; swollen portion 0.5–0.75 cm. long, with little or no declination.

It appears from these experiments that the tightly rolled cigarette gives slightly the more toxic smoke, though not markedly

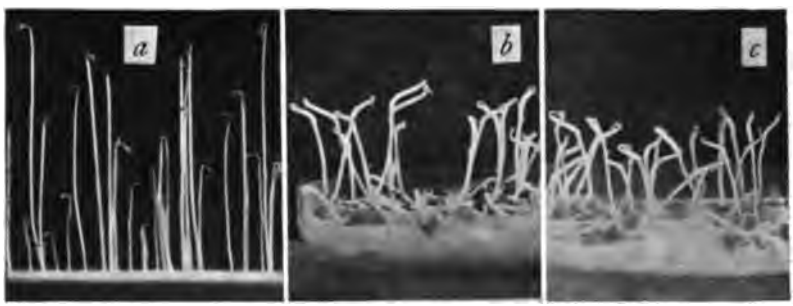

FIG. 2.—Responses to paper smoke: *a*, check; *b*, response to 10 cc. of smoke from loosely rolled paper cigarette in 10-liter chamber; *c*, response to 20 cc. of smoke.

so. In both sorts of smoke 10–20 cc. in 10 liters gives NELJUBOW'S third response, while 50 cc. in 10 liters gives his second response. It is apparent that considerable variation in concentration is necessary before a noticeable difference in response is shown. Even doubling the concentration may modify the response only slightly. This condition holds for ethylene, carbon monoxide, and a number of other gases, as our later paper will show. On the other hand, with pyridine, ethyl and propyl alcohol, acetylene, and others, rather slight variation in concentration is evidenced by very noticeable differences in the response. A series of photographs will give a more vivid idea of the response to smoke. Figs. 2 and 3 show the response to various concentrations of paper smoke.

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Experiment IV.—Effect of bromine absorption on the toxicity of paper smoke

In this experiment the washed smoke from the loosely rolled paper cigarette was absorbed with bromine by the gas analysis method described by HEMPEL. All traces of bromine were later absorbed by washing with 40 per cent NaOH. As is well known, bromine absorbs the heavy hydrocarbons (acetylene, ethylene, etc., with their higher homologues). It does not absorb methane or carbon monoxide. If the substance determining the toxicity of this smoke is one of the heavy hydrocarbons, this treatment should reduce the toxicity. If it is carbon monoxide or methane, it should not greatly modify the toxicity. The cultures were sealed in 10-liter chambers and subjected to the various sorts and concentrations of smoke for three days. The data show the condition of the epicotyls at the close of the experiment.

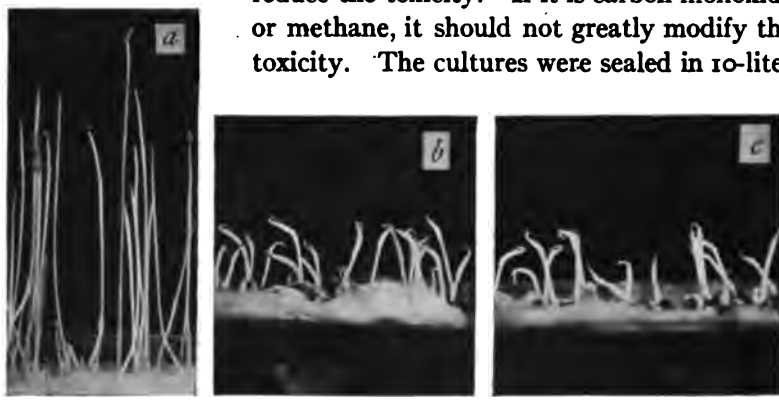

FIG. 3.—Responses to paper smoke: *a*, check; *b*, response to 20 cc. of smoke from tightly rolled paper cigarette in 10-liter chamber; *c*, response to 50 cc. of smoke.

1. Check; epicotyls 5–11 cm. tall, vertical and slim.
2. 20 cc. washed smoke not absorbed with bromine; epicotyls 3–4.5 cm. long; swollen portion 1–1.5 cm. long, with declination of 75°–90°.
3. 25 cc. (duplicates) washed smoke absorbed with bromine; epicotyls 6–12 cm. tall, vertical and slim.
4. 85 cc. washed smoke absorbed with bromine; epicotyls 4–9 cm. tall, vertical and slim.
5. 69 cc. washed smoke absorbed with bromine; epicotyls 4–9 cm. tall, slim and straight.

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6. 92 cc. washed smoke absorbed with bromine; epicotyls 3–7 cm. long; no swelling and little declination.

7. 550 cc. washed smoke absorbed with bromine; epicotyls 3–5 cm. long; swelling 2–3 cm.; declination 10°–60°.

It is evident from this series of cultures that absorption with bromine greatly reduces the toxicity of paper smoke and shows that substances belonging to the heavy hydrocarbons are the ones determining the toxic limit. The response given with 550 cc. of bromine-washed smoke is probably due to the CO, for that amount of smoke contains about 82 cc. of CO.

Experiment V.—The effect of coal smoke

The smoke was withdrawn from the furnace of a large flat building on a cold day, when large volumes of soot-free air were pouring from the chimney. The smoke showed the following analysis.

Volume analyzed	93.6 cc.	99.3 cc.
After NaOH	92.2	97.6
Difference = $CO_2 + SO_2$	1.4	1.7
	92.2	97.6
After phosphorous	75.8	80.2
Difference = O_2	16.4	17.4
	75.8	80.2
After ammoniacal cuprous chloride	75.6	79.9
Difference = CO	0.2	0.3

This smoke contained about 1.6 per cent of CO_2 and SO_2 together; long storage over water had probably reduced somewhat the percentage of these gases. The oxygen was reduced to a little less than 18 per cent, while only a trace of CO was present.

The following data report the results from exposing the test seedlings to various concentrations of this smoke. Part of these cultures were run in water-sealed bell jars and part of them in cans. At the beginning of the experiment the epicotyls were 2–3 cm. long, and after every exposure were slim and straight.

1. Control; epicotyls 6–12 cm. tall.
2. 20 cc. in 10-liter chamber; epicotyls 6–13 cm. tall.

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3. 50 cc. in 10-liter chamber; epicotyls 6–13 cm. tall.
4. 500 cc. in 10-liter chamber; epicotyls 5–10 cm. tall.
5. One liter in 10-liter chamber; epicotyls 4–9 cm. tall.
6. Three liters in 6 liters; epicotyls 3–7 cm. tall.
7. Two liters in 6 liters; epicotyls 3–7 cm. tall.

It is evident that the chimney smoke is very slightly toxic. In one-half an atmosphere of this smoke the epicotyl is less inhibited in growth than in one part in 1000 of the smoke from the loosely rolled paper cigarette. This shows that the latter smoke is more than 500 times as toxic as the coal smoke used. In commercial furnaces it is customary to supply just enough air to oxidize completely all gases. Any considerable excess adds to the volume of heated air passing out of the chimney and to an economic loss from this source. It is in this that the flat-owner can be criticized rather than the point in question, the addition of poisonous carbon-bearing gases to the air, for his furnace was receiving about 10 times the volume of air necessary to give complete combustion. High oxygen supply probably accounts for the small amount of reduced carbon-bearing gases and for the low toxicity of the smoke. It is an open question in commercial furnaces, where there is little excess of oxygen, whether there is a sufficient amount of these gases to play any part in the injury of vegetation, as SEARLE (41) has suggested. In general, the injury from coal smoke has been attributed entirely to tars and the oxides of sulphur. It is certain, however, that carbon-bearing gases, especially ethylene, might be in sufficient concentration to do injury and still be in too small quantities for detection by chemical methods (14, p. 257). A full discussion of this point is given in the last section of this paper.

Effect of the various constituents of smoke

The experiments already recorded afford evidence that the heavy hydrocarbons determine the toxic limits of tobacco and paper smokes. It is desirable, however, to know the magnitude of toxicity of the several constituents, also the nature of the response produced in the epicotyl by each. Moreover, it is desirable to determine the particular hydrocarbon responsible. For paper smoke this will demand the study of ethylene, propylene, acetylene,

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methane, and carbon monoxide, and in tobacco smoke pyridine, ammonia, hydrocyanic acid, and nicotine in addition, leaving entirely out of consideration the tars which have a relatively low toxicity where only their vapors are involved, and probably no such a magnitude of toxicity under any conditions as several of the carbon-bearing gases. Of these substances we will give detailed experiments only on carbon monoxide, hydrocyanic acid, and nicotine. For the other substances it will suffice merely to cite a portion of a table to appear in one of our later papers, along with the details from which it is derived. We consider the details on carbon monoxide here because it is the more abundant toxic gas and because MOLISCH suggests that it may be the one rendering the smoke so toxic to seedlings.

Experiment VI.—Effect of carbon monoxide

It is first desirable to make sure that the carbon monoxide used is free from the noxious gases, or at least that the effect produced is due to the contained CO and not to some impurity. For this reason the carbon monoxide was generated by three different methods and the three products compared as to their effects. It is assumed that if equal amounts of the three sorts of gas produce equal effects, the effect is due to the CO and not to impurities. Since the heavy hydrocarbons are so toxic, it was thought well to see whether washing the CO in bromine would reduce the toxicity.

When oxalic acid was heated with several times its weight of concentrated H_2SO_4 and washed with 40 per cent NaOH, a gas resulted which gave (duplicate analysis) 99 per cent absorption with ammoniacal cuprous chloride. Potassium ferrocyanide was heated with 8–10 times its weight of concentrated H_2SO_4 and washed with 40 per cent NaOH. In duplicate this showed 96 per cent CO. Sodium formate was heated with concentrated H_2SO_4 and produced a gas giving 89 per cent absorption with ammoniacal cuprous chloride.

The epicotyls were 2.5–3.5 cm. tall at the beginning of the experiment and were inclosed in 10-liter cans. The following data show the sources and concentrations (correcting for impurities) of CO used, and the condition of the seedlings at the close of the experiment.

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1. Check; epicotyls 6–11.5 cm. tall, vertical and slim.

a) Potassium ferrocyanide-derived CO

2. 50 cc.; epicotyls 4–6.5 cm. long, with declination of 20°–45°; no swelling, but larger diameter than checks.

3. 100 cc.; epicotyls 3–5 cm. long; swelling 1–2 cm. long, with declination of 70°–90°.

4. 200 cc.; epicotyls 2.5–4.5 cm. long; swelling 1–1.5 cm. long, with declination 80°–90°.

5. 100 cc. washed in bromine; epicotyls 3–5.5 cm. long; swelling 1–2.5 cm. long; declination mostly 30°–60°.

6. 200 cc. washed in bromine; epicotyls 2.5–4 cm. long; swelling 1–2 cm. long; declination 60°–90°.

b) Oxalic acid-derived CO

7. 50 cc.; epicotyls 4–7.5 cm. tall; no swelling, but diameter larger than checks; declination 25°–35°.

8. 100 cc.; epicotyls 3–5.5 cm. long; swelling 1–2.5 cm. long; declination 60°–90°.

9. 200 cc.; epicotyls 3–5 cm. long; swollen zone 1–1.5, with declination 75°–90°.

c) Sodium formate-derived CO

10. 50 cc.; epicotyls 5–7 cm. long; no swelling, but declination 15°–40°.

11. 100 cc.; epicotyls 4.5–5.5 cm. long, with swelling 1.5–2.5 cm. long, and declination 60°–90°.

12. 200 cc.; epicotyls 3–5 cm. long; swollen zone 1–2 cm., with declination 70°–90°.

A series of photographs will show the response to CO (oxalic acid-derived) of various concentrations (fig. 4). It is evident that the responses obtained in this experiment are due to the CO contained in the gases and not to impurities. When the data and figures on CO are compared with those on smoke from paper cigarettes, it is seen that the smoke is about 10 times as toxic as pure CO; 10 cc. of the smoke give responses similar to 100 cc. of CO, and 20 cc. of the smoke similar to 200 of CO. Since the smoke is approximately 15 per cent CO, it contains only about $\frac{1}{60}$ enough CO to determine its toxicity. This helps to substantiate the conclusion that the heavy hydrocarbons determine the toxic limit of paper and tobacco smoke, so far as the plant organ studied is concerned.

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Various amounts of nicotine (1–30 drops) were placed on filter papers and sealed in 10-liter cans with cultures. Only the smaller amounts completely volatilized, but in none was any inhibition of growth noticeable. The test seedlings in culture cans of various sizes, bearing several grams of pulverized KCN, showed no inhibition of growth. In this connection it should be stated that HCN exists in such small quantities in tobacco smoke (0–60 mg. from 100 gm. of tobacco) that LEHMANN (18) does not take it into consideration as a toxic factor with the smoker. It is certainly much less to be considered in plants to which it is rather slightly toxic.

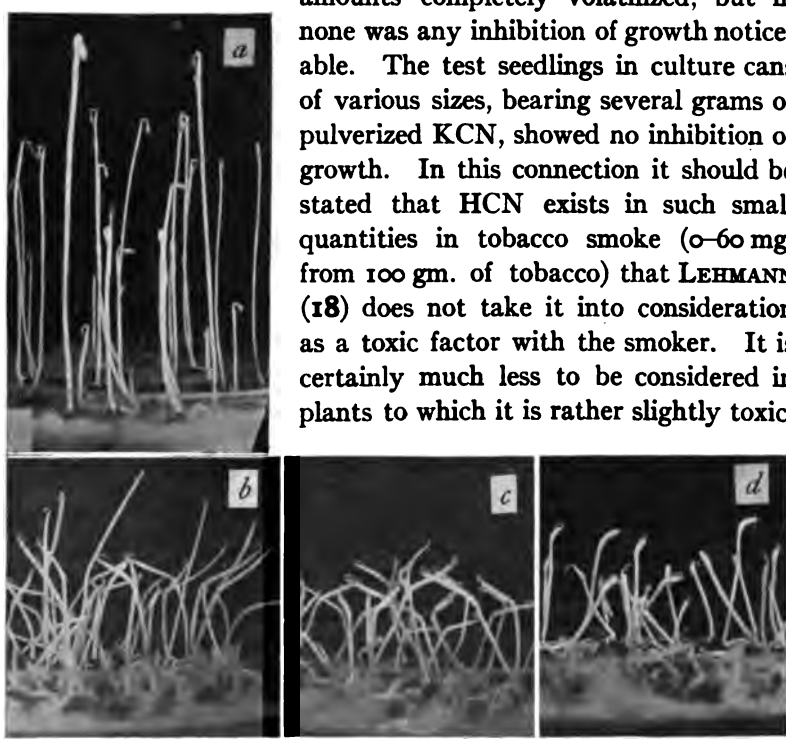

FIG. 4.—Responses to CO: *a*, check; *b*, 50 cc. of CO in 10 liters; *c*, 100 cc. of CO in 10 liters; *d*, 200 cc. of CO in 10 liters.

The following table (p. 362) shows the nature of the responses caused by other constituents of tobacco and paper smoke and the concentrations necessary to produce them.

In this table inhibition of growth corresponds to the sixth response of NELJUBOW, declination to the fifth, and horizontal nutation and swelling to the third. Only 4 of the 30 or more common gases and vapors whose effect on this organ we have studied certainly produce "declination" or "horizontal nutation and swelling." They are ethylene, acetylene, propylene, and carbon monoxide. This does not include the mixtures of gases (illuminating gas

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and various smokes) in which the response is quite certainly due to one of these constituents. It also omits methane, for which it is not yet certain whether the response produced by the very high concentration given above is due to methane or to impurities. This uncertainty exists because methane derived by three different methods gave extremely great differences in magnitude of toxicity, though analyses showed the three sorts to contain approximately the same percentages of methane. At most, methane is very slightly toxic, if indeed further experiments do not prove it entirely harmless.

Gas used	Parts per million of atmosphere to produce		
	Inhibition of growth	Declination	Horizontal nutation and swelling
Ethylene	0.1	0.2	0.4
Acetylene	100.0	250.0	500.0
Propylene	75.0	1000.0	1000.0
Carbon monoxide	5000.0	5000.0	10,000.0
Methane	60,000.0?	200,000.0?	500,000.0?
Pyridine	300.0	None	None
Hydrogen sulphide	500.0	None	None
Ammonia	3000.0	None	None

The nature of the response (triple response) of the seedling to paper and tobacco smoke shows that it must be caused by one of the four carbon-bearing gases mentioned above or by homologues of some of them. Before going into the probability as to which of these determine the effective limit of the smoke, let us consider the concentrations of other constituents in unwashed tobacco smoke and the chances that they may play some part, at least, in the inhibition of growth, in experiments such as reported in this paper or those performed by MOLISCH.

According to LEHMANN (18) 100 gm. of tobacco when smoked in a pipe or as a cigar produces about 16 cc. of H_2S. In experiment II (3) in which the smoke from 0.0375 gm. of cigar is placed in a 50-liter can, NELJUBOW's third response appears. The H_2S content in this experiment, if it had not been washed out, would be 1 part in 8 million of atmosphere, or about 0.0002 sufficient to reduce growth. According to the same worker, 100 gm. of tobacco when thus smoked produces 0.935 mg. of NH_3. In experiment II

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(3), according to these figures, if the smoke had not been washed, ammonia would have been present in the proportion of 10 parts per million of atmosphere, or in about 0.003 sufficient concentration to inhibit growth. Pyridine exists in very small quantities in tobacco smoke, certainly far below amounts that would inhibit growth in experiment II (3).

Both the nature of the response of the seedling and the concentration of the smoke necessary to produce it indicate that one of the four carbon-bearing gases mentioned above or homologues of some of them fix its toxic limit. We have shown that it cannot be carbon monoxide on account of insufficient quantities of that substance. In what percentages of the smoke must the others exist to determine its toxicity? Let us consider experiment III (2) of washed smoke of the loosely rolled paper cigarette, almost as toxic as any tested. In this case it required 10 cc. of the smoke in 10 liters to give NELJUBOW's third response, or the response listed in the table above as "horizontal nutation and swelling." Using the figures in the table above as the basis for calculation, ethylene must be present in 0.04 per cent, acetylene 50 per cent, and propylene 100 per cent of the smoke, to determine its toxicity. In experiment III (2) under discussion, the heavy hydrocarbons were not in sufficient concentration to be detected by the gas analysis methods used, which should easily detect 0.2 per cent. If one of these three gases is responsible, it must be the ethylene. In short, the sweet pea seedling will give the triple response in concentrations of ethylene 0.001–0.002 sufficient to be detected by gas analysis methods, while it will respond by reduced growth in concentrations 0.0003 to 0.0005 sufficient to be thus detected.

It is possible that in tobacco burned in the open, as is done when using it as an insecticide in greenhouses, the ammonia is produced in larger quantities as compared with the heavy hydrocarbons, and that ammonia much more nearly approaches the toxic limit. We have already shown that paper burned as a cigarette produces smoke 50 times as toxic as when burned as an open sheet. This means a great fall in the production of heavy hydrocarbons under conditions of high oxygen supply. There is probably also less ammonia produced when the aeration is better, for LEHMANN

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(18) found that in cotton cigarettes impregnated with nitrates much of the nitrate nitrogen was reduced to ammonia nitrogen. Such reductions likely occur to a much slighter degree under better conditions of aeration. Similar conditions may hold for hydrogen sulphide.

V. General considerations

In the destructive distillation gases from carbon compounds, whether we consider smoke or illuminating gas, the preponderant toxicity of the heavy hydrocarbons, especially ethylene, is very interesting. The present paper shows this relation to hold for the sweet pea epicotyl, while a former paper pointed out the same situation for the carnation flower. Mr. E. M. HARVEY of this laboratory has shown that the ethylene in illuminating gas determines the toxic limit of that mixture to the roots of *Vicia Faba*, though in this case the magnitude of toxicity is much less than in the cases of the two plant organs mentioned above. In the light of the facts set forth in this paper, it becomes probable that the extreme toxicity of smoke for seedlings observed by MOLISCH (22) can be attributed to the heavy hydrocarbons. It is as yet unanswered whether the nocuous character of smoke to various microorganisms, and to the organs of mature angiosperms as observed by this writer, is due to the same constituent. Whatever be the case, it is clear that some plants are quite resistant to the destructive distillation gases of carbon compounds, as MOLISCH states and as RICHARDS and MACDOUGAL (31) have found. To what degree the resistance is due to protective structure or permeability characters and to what degree to peculiarities of the plasma cannot be stated.

It is probable that production of the toxic materials from carbon compounds begins considerably before the lower temperature limit set for destructive distillation is reached. In soils it was found in this laboratory that heating but slightly above 90° C. for an hour liberated substances that produced the "triple response" in the pea epicotyl. Mr. HARVEY is now making a study of the gases liberated from soils when heated at various temperatures. It is evident that contact of hot steam pipes with soil in greenhouses

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may produce gases very toxic to plants. Whether they are likely to reach sufficient concentration to do injury is not determined.

Injuries from coal smoke are generally attributed to tars and oxides of sulphur (**3, 4, 7, 40,**), while reduced carbon-bearing gases have never been considered as a factor. According to HEMPEL (**14**, p. 257), these gases, especially the heavy hydrocarbons, exist in such small quantities, if at all, even when the oxygen supply is very little more than enough to produce complete oxidation, that they cannot be detected by gas analysis methods. This does not mean that they can be neglected as a source of injury to vegetation, for, as we have shown, growth rate is reduced in the pea epicotyl in 0.0003–0.0005, the least concentration of ethylene detectable by gas analysis methods. In short, while the gas analysis methods are quite adequate for guarding against considerable energy loss due to incomplete combustion of heavy hydrocarbons in furnaces, the only way to make sure that they are not in sufficient concentration to do injury to vegetation is to use a more delicate test, such as the pea epicotyl.

One factor that favors the effectiveness of the oxides of sulphur as plant poisons in the open as against heavy hydrocarbons is their great solubility in the plant cell, which would lead to their accumulation even under great variation in the atmospheric concentration, whereas the heavy hydrocarbons will accumulate to a far less degree, and variations in concentration greatly reduce their injurious effects. It is probable that smoke from the beehive coke oven is much richer in heavy hydrocarbons than furnace smoke, especially in the early firing (**2**). Part of the destruction of vegetation about these may be due to the carbon-bearing gases, though here, as in furnace smoke, there is an abundance of sulphur dioxide and tars. The economic loss through injury to vegetation is probably rather slight, because of the nature of the region in which this industry is carried on. It certainly is inconsiderable beside the $44,000,000 worth of products this wasteful method of coking is pouring into the atmosphere annually in the United States alone (**19**).

Artificial illuminating gas is a source of great economic loss through injury to plants. A large number of cases of injury to greenhouse stock in different parts of the country have been called

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to our attention. As we have already pointed out (6), these losses generally occur during cold periods in winter. This insures a frozen crust, promoting lateral diffusion of the gas from the faulty mains; it also prevents ventilation of the greenhouses. So far as evidence for the constituents that produce the injury goes, it suggests the heavy hydrocarbons, though it is not by any means proved that these are responsible for all such injuries. A source of greater loss from illuminating gas is injury to shade trees. This injury is through the roots, in contrast to the injury in greenhouses. We are unable to state as yet what constituents produce the injury, though Mr. HARVEY's work in this laboratory indicates that ethylene determines the toxic limit of the gas for the roots of *Vicia Faba*. Even so, it is possible that the less volatile materials of the gas accumulating in the soil may really be the source of injury, the power of accumulation overbalancing the higher toxicity. The determination of the constituents producing the injury and the tenacity with which they adhere to the soil are of great importance. They determine how soon and under what conditions replacing of the dead trees by new ones can be carried out. Mr. HARVEY is now attempting to answer these questions. The odor-producing substances of illuminating gas are retained in the soil with great tenacity, but so far as the pea epicotyl is concerned, these substances are innocuous, at least in concentrations easily detected by smell. Natural gases are generally low in heavy hydrocarbons; in fact, those of the Appalachian system bear none so far as chemical tests indicate (1); they consist mainly of methane and ethane. This gas should be very low in its toxicity to plants. The Baku natural gas is said (30) to contain some olefines.

The few facts established in this field suggest the need of rationalizing various practices in vogue and summarily abolishing others; for instance, the practice of burning tobacco stems in greenhouses for killing insects. This is a matter of differential poisoning, applying a poison that will kill the insect without injuring the plants. The processes volatilize nicotine and set free carbon monoxide, ethylene, and other gases. So far as we know, it is not certain which is the insecticide. If it is nicotine, why not volatilize nicotine from an extract and avoid the deadly plant poison ethylene?

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If it is carbon monoxide, why not generate it chemically and thereby avoid ethylene? Again, it is a rather common practice to have the heating furnace in more or less open connection with the greenhouses. If one recognizes the probability of the dry distillation gases escaping from a furnace, along with the extreme toxicity of ethylene, he can see the need of abolishing this practice.

So far as known, the etiolated epicotyl of the sweet pea is the most sensitive plant organ to ethylene. As has been stated, it is inhibited in growth by 1 part in 10,000,000 of atmosphere. The open flower of the carnation is only a little less sensitive. In our original measurements (**6**), which were made on plants that had been bearing flowers for several months, 1 part in 2,000,000 of atmosphere "put the open flower to sleep" in 12 hours. Some later measurements with plants soon after they had begun to flower showed that 1 part in 3,000,000 of atmosphere caused the same response. While the open flowers on these younger plants were much more sensitive to ethylene, the buds proved much more resistant than the buds of plants longer in bearing.

If, in the few cases tested, two such sensitive plant organs have been found, it is probable that many more exist. So far as we know, there is in nature no special absorbent for ethylene, also no cycle for the gas, as there is for carbon dioxide and oxygen. Even if both existed, one doubts if 1 part in 10,000,000 would lead to a withdrawal. Processes of civilization are continually adding to the ethylene in the atmosphere, as burning of all carbohydrates, burning of coal (?), escaping of artificial illuminating gas, producing of gas in the beehive method of coking, escaping of certain sorts of natural gas, and probably other processes. Having no estimate of the total additions from these sources, one cannot calculate whether accumulation in the atmosphere up to a danger point is likely to occur.

The etiolated epicotyl of the sweet pea is a very delicate test for the heavy hydrocarbons, especially ethylene. One of the papers to be published later will show that under proper application it is also a very reliable test for this group of substances. It could be used to determine the presence or absence of this group of gases in coal smoke, gas from coal (**28**), and natural gas, where gas

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analysis methods are inadequate. To the experimenter in plant physiology it furnishes an excellent means of making sure that the laboratory air is sufficiently "pure" not to interfere with plant response, while to the practical greenhouse man it furnishes a means of determining the probability of injury from illuminating gas or other mixtures bearing ethylene.

Summary

1. The smoke from tobacco cigars and cigarettes which has been thoroughly washed in 15 per cent H_2SO_4 and 40 per cent NaOH is very toxic to the etiolated epicotyl of the sweet pea. In the case of cigar smoke thus treated, 1000 parts per million of atmosphere give a triple response: reduction of rate of elongation, swelling, and diageotropism of the portion growing in the impurity; 5000 parts per million of atmosphere completely stop elongation and produce a swollen knob, while the epicotyl remains vertical; still higher concentrations kill the epicotyl before any form change occurs.

2. On the basis of dry weight burned, the washed smoke from cellulose paper cigarettes is even more toxic. The characters of the responses produced are identical with those produced by smoke from tobacco cigars and cigarettes.

3. When smoke from equal amounts of cellulose paper, smoked as a cigarette on one hand, and burned as an open sheet on the other, are compared, it is found that the former is 50 times as toxic as the latter. Higher oxygen supply during burning greatly reduces the toxicity. A large part of the toxic gases are undoubtedly oxidized to CO_2 and H_2O.

4. In the cigarette smoke of cellulose paper the following gases are present: carbon dioxide, carbon monoxide, acetylene, ethylene, methane, and some higher homologues of the last three. Washing out the carbon dioxide does not reduce the toxicity of the smoke, nor will carbon dioxide produce the type of response produced by the smoke. Carbon monoxide, acetylene, ethylene, propylene, and perhaps methane produce the same type of response as smoke. Carbon monoxide is in 0.015 sufficient concentration to determine the effect of smoke. It is not certain that methane is toxic at all;

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if so, it is not in 0.00001 sufficient concentration to produce the response. The other three gases mentioned are not present in the smoke in sufficient quantities to be detected by ordinary gas analysis methods. Considering the magnitude of toxicity of acetylene and propylene, it is impossible that they play any part in the toxicity of paper smoke. The great toxicity of ethylene makes it probable that it determines the toxic limit. One part of ethylene in 10,000,000 of atmosphere inhibits elongation of the epicotyl, 4 parts in 10,000,000 produce the triple response. The toxicity of paper smoke is greatly reduced by washing with bromine, which is further evidence that ethylene or some other heavy hydrocarbon is the effective gas.

5. In addition to these gases, tobacco smoke bears hydrogen sulphide, ammonia, nicotine, hydrocyanic acid, and pyridine. None of these produces the type of response in the seedling caused by the smoke, and they exist in the smoke in concentrations far below that necessary to determine the toxic limit. The facts stated in this paper, along with the work of MOLISCH and others, show the hazard of using tobacco smoke as an insecticide for greenhouses.

6. The etiolated epicotyl of the sweet pea is a very delicate test for the heavy hydrocarbons (ethylene), exceeding many fold the delicacy of any chemical test.

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WESTERN PLANT STUDIES. I

AVEN NELSON AND J. FRANCIS MACBRIDE

[The last four numbers of "Contributions from the Rocky Mountain Herbarium" (IX–XII) were based largely upon the collections made by Mr. J. FRANCIS MACBRIDE in 1910 and by MACBRIDE and myself in 1911. During the season of 1912, the field work was continued by MACBRIDE assisted during a part of the time by Mr. DORMAN BENNITT and by the writer. The territory covered was a small part of southwestern Idaho and certain parts of Nevada in and adjacent to the Humboldt National Forest. Our work in Nevada was greatly facilitated by the kindly assistance of the Forest Service, and we wish to acknowledge gratefully the many courtesies extended by Supervisor C. SIDNEY TREMEWAN and his assistants and foresters. The types, the numbers of which are given, were all collected by NELSON and MACBRIDE and are deposited in the Rocky Mountain Herbarium.

In working up the collections of 1912, Mr. MACBRIDE has been associated with me, and the paper presented herewith is the result of this collaboration. This and other papers that we may publish jointly will be under the above title; while those for which I individually assume responsibility will be continued as "Contributions, etc."—AVEN NELSON.]

Calochortus bruneaunis, n. sp.—Stems striate, minutely scabrous in lines, especially near the base, 2–4 dm. high, more or less tortuous: bulb narrowly oblong, covered with brown, dead scales, as is also the base of the stem: leaves several (4–6); the radical leaf nearly or quite equaling the plant; the cauline involute, expanded and scarious-margined at the sheathing base, 4–10 cm. long: flowers 1–3, axillary in the upper leaves: sepals rather broadly lanceolate, 2–3 cm. long, tapering gradually to a slender tip, colored like the petals within, green without but with a broad white scarious margin to above the middle: petals broadly obovate-cuneate, rather abruptly rounded above into a blunt point, longer than the sepals; body-color white, delicately streaked with green, with a green band from apex to the narrow yellow claw, just above which is a small purple inverted V-shaped or lunate blotch: petal wholly glabrous, even the small oblong gland at the summit of the short claw scarcely pubescent: anthers obtuse, purple, 6–8 mm. long, about equaling the filaments: capsule narrowly oblong.

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This makes the third species in the green-banded group, the others being *C. cyaneus* A. Nels. and *C. macrocarpus* Dougl. The latter is the nearer relative to the species now proposed. *C. bruneaunis* is easily distinguished by the rather tortuous stems, the different color and marking of the flowers, and the glabrous petal faces.

No. 1881, found in chipped lava, high on the canyon sides of the "Hot Hole" of the East Bruneau, Owyhee County, Idaho, is the type.

Clematis aurea, n. sp.—Glaucous, climbing freely by the petiolules: stems glabrous, striate: leaflets broadly to narrowly lanceolate, petiolate, pale green, irregularly incisely dentate, acuminate-cuspidate, midvein prominent beneath: bud green, drooping, erect in anthesis, the four sepals then golden yellow, 4–5 cm. long, oblong, obtuse, cuspidate, rather thick, prominently nerved, glabrous except for an incurved villous margin: the pubescent filaments dilated, 8–10 mm. long, all antheriferous; anthers linear, about 5 mm. long, obtuse, minutely cuspidate: achenes pubescent, the persistent black styles filiform, only moderately white plumose throughout, 4–5 cm. long.

Collected in July 1909, at Challis, Custer County, Idaho. It was locally plentiful, clambering over rosebushes, etc., along a stream, and attracted attention by its unusual color and beauty. It is a member of the section VIORNA, though with sepals scarcely leathery. In aspect the plant more nearly resembles some members of the section ATRAGENE.

Delphinium megacarpum, n. sp.—Much resembling *D. Andersonii* Gray, having a similar fascicle of long thickened woody roots and a strict mostly simple few-leaved stem: basal leaves petioled, from puberulent to nearly glabrous, suborbicular in outline, cuneately divided or parted, the lobes cleft into linear divisions; the stem-leaves rather remote, gradually reduced in size and number of lobes, puberulent or more usually sparsely hirsute-ciliate, the bracts and base of petioles conspicuously so: stems rather stout, 2–5 dm. high, at first cinereous-puberulent to the base, becoming glabrate below in age: inflorescence narrow, racemose and usually with one or more slender erect floriferous branchlets from the uppermost axils: flowers dark blue: calyx softly hirsute, spur longer than the sepals and these exceeding the petals: carpels puberulent even at maturity, linear-oblong, 20–25 mm. long, erect and parallel,

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only the tips divaricate, reticulately veined: seed-body large, dark, narrowly winged on the margins and with a depressed summit.

This species has passed for *D. Andersonii* and is a close relative of it. The typical form of that seems to be confined to western Nevada and adjacent California. Taking those characters on which Dr. GRAY laid stress, namely, "very glabrous"; "follicles oval or oblong, not over half an inch in length"; "seed body small and broadly winged," as diagnostic, one is almost forced to separate this pubescent long-carpelled form. The segregate occurs in interior northern Nevada, Idaho, and adjacent Oregon. No. 1779, House Creek, Idaho, June 29, 1912, is the type number.

ARABIS MENZIESII **lata**, n. var.—Closely allied to the species, but the pods broader (as much as 6 mm.), 2.5–4.5 cm. long, usually about twice as long as the pedicels; style nearly wanting.

As shown in Proc. Biol. Soc. Wash. **17**:91 and **18**:187, the PHOENICAULIS section of *Parrya* is less aberrant in *Arabis* than in *Parrya*. Typical *Arabis* (*Parrya*) *Menziesii* will not run to *Parrya* by any of the keys to the cruciferous genera, but does run to *Arabis* by most, if not all, of such keys. The variety here described is probably the *P. Menziesii* of Bot. King Rep. 14, in part.

Fully mature material is our no. 1838, from lava cliff pockets, House Creek, Idaho, June 30, 1912.

ARABIS PEDICELLATA A. Nels., Proc. Biol. Soc. Wash. **17**:91 is *Parrya Menziesii lanuginosa* Wats., and may best become ARABIS MENZIESII **lanuginosa**.

Horkelia beneolens, n. sp.—Caudex simple or branched, more or less fleshy or becoming woody, thick because of the dense coat of dead brown petioles, the flaccid sordid herbage clammy with a short glandular pubescence: stems few–several from each crown, sparingly leafy, 7–15 cm. long including the rather open inflorescence: leaves several from each crown, mostly oblong, with 5–9 pinnae, on slender petioles: pinnae 7–15 mm. long, alternate or irregularly opposite, oblong, flabelliform or suborbicular, more or less deeply palmately parted into oblong obtuse or acutish lobes; stem-leaves short, with fewer pinnae (3–5) and short petioles (or subsessile); stipules ovate-oblong: flowers few–many on slender pedicels in an open cyme: calyx rotate, with flat pentagonal hypanthium with a marginal flange giving a sunken or inverted salver-form effect (as in the base of the calyx of some species of *Physalis* in fruit); lobes ovate, acute, about 3 mm. long, fully twice as long

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as the small linear-oblong bractlets: petals white, shorter than the lobes of the calyx, the small linear-lanceolate blade scarcely longer than the slender claw: stamens 5; the brown anthers subspherical, their cells opening lengthwise: pistils 3–5, sometimes all maturing: achenes large (2 mm. long), flattened, ovoid, with the inner edge nearly straight, noticeably longitudinally ridged on the surface.

This plant has the foliage of some of the sections of *Horkelia*, the numerical plan of certain species of *Ivesia*, while the calyx characters come nearest to *Comarella*. Unfortunately this cannot get into that genus since in it the petals are red and the pistils only two. On the whole the plant here described probably comes nearest to *Horkelia Baileyi* (Wats.) Rydb. The specific name chosen refers to the delightful fragrance emitted by the plant.

It does not seem possible to maintain these three genera in view of the increasing number of species that show characteristics that overlap the generic bounds. In fact, what character, except the open space between pistil-bearing receptacle and the margin of the hypanthial disk, separates any of them constantly from *Potentilla?* Agreeing in this one character and overlapping as to other characters, it is in the interest of simplicity to let *Horkelia* include them all.

No. 1708, Castle Ford, on the Salmon, in Idaho, is the type. It was found hanging in wet crevices on the vertical faces of basaltic cliffs, June 25, 1912.

POTENTILLA GLOMERATA **dichroa**, n. comb.—*Potentilla dichroa* Rydb. N. A. Fl. 22:319. 1908.

This is distinguished from the species only by the denser tomentum on the under side of the leaves and the grayer color of the plant as a whole.

Astragalus owyheensis, n. sp.—Spreading, prostrate, many-stemmed perennial, tufted at base, minutely and sparsely strigillose, the slender wiry stems, including the open racemes, 2–6 dm. long: stipules triangular, the lower about 3 mm. long and scarious, upward becoming smaller and green: leaves 6–10 cm. long, rather irregularly pinnate; the leaflets (5–13) remote, shorter than the internodes, linear: the very open axillary racemes exceeding the leaves: the slender pedicels 3–6 mm. long: calyx finely strigillose with intermingled black hairs, the subulate teeth about one-third as long: flowers 8–10 mm. long, white; standard 5 mm. wide, rather deeply emarginate, the edges strongly recurved, forming two crests at the edge near the middle of the blade: wings not emarginate, narrowly obovate, the edges incurved: keel shorter, with a broad

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rounded incurved apex: pod oblong-linear, pubescent like the plant, shortly acute, 10–18 mm. long, straight or slightly curved, usually recurved but sometimes ascending, one-celled, the dorsal suture being but slightly intruded: seeds few (about 5).

Perhaps this finds its nearest relatives in *A. atratus* Wats. and *A. obscurus* Wats. No. 1887, collected July 2, 1912, above the "Hot Hole" of the East Bruneau, Owyhee Co., Idaho, is the type. It was quite inconspicuous because of its color and its habit of creeping among the short grasses of the sagebrush plains.

GERANIUM CAESPITOSUM **gracile**, n. comb.—*G. gracile* Engelm. in Gray Pl. Fendl. 27. 1849; *G. atropurpureum* Heller, Bull. Torr. Bot. Club **25**:195. 1898; *G. furcatum* Hanks, N. A. Fl. **25**:16. 1907.

Specimens of *G. caespitosum* when they show a tendency to become glandular pubescent on the pedicels have been considered as *G. gracile* (*G. atropurpureum*), and if this glandulosity extends to the stem they are *G. furcatum*. A series of specimens can be so arranged as to show all degrees of glandulosity to the complete lack of it. The proposed variety, therefore, rests primarily upon the slenderer and more erect stems, the narrower petals, and usually a trace of glandulosity. Where the glandulosity becomes marked throughout, it merges into *G. Parryi* (Engelm.) Heller.

It is somewhat singular that there should be any misunderstanding in regard to *Geranium caespitosum* James. Admitting that the original printing of the name did not publish the species, Dr. GRAY's diagnosis in Pl. Fendl. 25 and Dr. TRELEASE's in Bost. Soc. Nat. Hist. **4**:72 fixed the plant to which this name must apply.

Specimens answering to this description are not rare in the herbaria and are always non-glandular and with the pubescence of the stem (whether sparse or abundant) more or less retrose. The plant is always cespitose, growing in the form of a turf or mat from which short assurgent stems arise. The new characterization in the N. A. Fl. **25**:15 would seem to be without warrant, and at best that description presents merely one of the variants of *G. Fremontii* Torr.

Specimens wholly typical of *G. caespitosum* are BAKER 448, Colorado; BAKER, EARLE, and TRACY 407, Colorado; 1155 from Colorado, distrib. by the New York Bot. Gard. as one of the type nos. of *G. Cowenii* Rydb.; BUFFUM, Wyoming; NELSON 8591, Wyoming; METCALF 194, New Mexico; MACDOUGAL 118, Arizona. Besides *G. Cowenii*, *G. marginale* Rydb. must undoubtedly be referred to *G. caespitosum* as here understood.

GENTIANA AFFINIS **major**, n. var.—Leaves uniformly narrower: calyx lobes oblong-lanceolate, nearly equal and all approximately

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equaling the tube: corolla broadly funnelform, larger, diameter at the top more than 2 cm.; the plaits purple, alternating with green bands extending downward from the lobes, the sinuses short.

This would be a good species if all degrees leading to the above characters were not present in a collection of *G. affinis*. Collected at Mountain City, Elko Co., Nevada, August 9, 1912, no. 2178.

Nemophila explicata, n. sp.—Branching from the base; the branches sometimes sparingly branched, 7–15 cm. long, spreading or weakly erect, glabrate, the scattering hairs short and refracted: leaves obovate or orbicular in outline, cuneately tapering into a margined petiole one-fourth to one-half as long as the blade, crenately 3–5-lobed, 10–20 mm. long, sparsely strigulose with more or less appressed hairs: pedicels 7–14 mm. long, at length more or less reflexed or even refracted: flowers small, not white; calyx appressed strigulose, in fruit 2 mm. or scarcely more long; its tube short; its lobes ovate, sparsely short ciliate on the margins, its appendages small, oblong, as long as the tube: corolla small, barely exceeding the calyx, tubular-campanulate, its oval lobesal most as long as the tube, the plicae or appendages wholly wanting: style short, divided at apex only: capsule 3–4 mm. long, more or less appressed cinereous-strigulose: seeds 4, large, 3 mm. long, irregular quadrants, slightly roughened, pale yellow with numerous small brownish dots or obscurely pitted; the membranous cellular caruncle caplike.

Secured at Jarbidge, in the canyon of the East Bruneau River, among shale-lava, growing with *N. breviflora* Gray. Only one other of the described species seems to be devoid of appendages in the corolla tube. No. 2229, July 7, 1912, is the type.

Phacelia foliosepala, n. sp.—Slender annual, 7–12 cm. high, hirsute-pubescent and glandular, trichotomously branched (candelabra-like) twice or thrice, the branches usually simple, floriferous to near their bases: leaves few, scattering, 1–1.5 cm. long, oblanceolate, obtuse, tapering below to a short margined petiole: inflorescence racemose, rather open in fruit (flowers unknown): pedicels about 2 mm. long: calyx lobes foliar, unequal, resembling the leaves, 10–15 mm. long, more than twice as long as

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the capsule: capsule oval: seeds 12, irregularly ellipsoidal, beautifully alveolate, seal brown when mature.

Possibly this may best be referred to the section EUTOCA Gray, but even in this section there seems to be no species nearer to it than *P. linearis* (Pursh) Holz. That, however, is a very different plant in its mode of branching, in its different and glandless pubescence, and probably in all of its floral parts as it evidently is in its calyx. It is interesting that this little annual possessed (according to the field notes) a "strong vile odor, something fierce," reminding one of those perennials like GOODDING'S *P. foetida* that proclaim their identity while they are still a long way off.

The type is no. 2232, Gold Creek, Nevada, July 27, 1912; moist sunny flat.

Oreocarya cilio-hirsuta, n. sp.—Biennial or, apparently, sometimes perennial, from a slender taproot more or less branched at summit; the branches of the caudex or crown short and clothed with the inordinately crowded linear leaf-bases: stems several–many, very slender, somewhat angled, greenish but thinly hirsute and with an admixture of long white stiff ciliate-appearing hairs, 15–30 cm. long and floriferous in the axils for half their length: crown leaves very numerous, 2–4 cm. long, linear, the upper part more or less spatulate and not more than half as long as the slender petiolar portion; cauline shorter, mostly broadly linear; all with pubescence similar to that of the stems: the rather small axillary thyrsoid clusters 10–15, crowded above, more open below and usually surpassed by the foliar bracts: inflorescence moderately hirsute-hispid: calyx lobes linear-lanceolate, 6–8 mm. long in fruit: corolla tube barely as long as the calyx, its lobes suborbicular, half as long as the tube: nutlets ovate as to the body but narrowed and subacute at apex, bordered by a filiform wing-margin, sparsely but sharply muriculate on the back, even more minutely on the ventral side, not at all rugulose; scar linear, nearly as long as the nutlet, slightly enlarged at the base but not forked.

The type is no. 1799, from Minidoka, Idaho, June 23, 1912, where it was growing in the loose sagebrush soil. MACBRIDE'S no. 93 from New Plymouth, May 21, 1910, and his no. 875, from Sand Hollow, June 2, 1911, were distributed as *O. affinis* and *O. affinis perennis* respectively. Neither of these accord very closely with the species to which they were referred, and although not identical with the species here proposed, they will probably have to be considered a part of it rather than of *O. affinis*.

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CASTILLEJA MINIATA Dougl.—Special effort was made to secure as full a series as possible in this genus in order to see something of the degree of variability within specific lines. No species shows how great this variability is better than *C. miniata*. Incidentally it may be remarked that the making of synonyms is not always due to the variability in the specimens representing a species, but quite as often to errors in the original descriptions which authors continue to copy and with which we constantly compare new material. Another source of error is found in the habit, more or less prevalent, of naming up material by comparison alone. *A* has a specimen slightly aberrant; *B* names his by comparison with *A*'s, and lets it pass though evidently somewhat different; *C*, having *B*'s plant, names his material accordingly, and so on. Look through any well filled species cover and see these facts illustrated.

In the original description of *C. miniata* the galea is said to exceed the corolla tube. On the assumption that this was so for the species (it probably was on the type sheet) some segregates have been made by various authors that had better not have been made. *C. miniata* material measured by this yardstick contains few (if any) specimens that are typical. Dr. RYDBERG, for example, in working all the material for his *Flora of Montana* had but one number (RYDBERG and BESSEY 4965, Wolf Creek, 1897). Unfortunately, too, other sheets of even this same number (4965) show only corollas in which the galea is shorter than the tube. The character is therefore more or less unreliable in this species, and hence probably in others.

Another character in *Castilleja* which is often misinterpreted is the root system. Collectors almost always pull the stems loose from the root or caudex. Being usually numerous in the clumps they are decumbent at base, and more or less rooted at the lower nodes. This often gives them the appearance of having been detached from a running rootstock when such was not the case.

Of course it is generally known that the color of the bracts varies, and this gives the plants a very different look even when the color of calyx and corolla remains (as it should) fairly constant.

These observations were induced by the necessity of distributing several of our numbers as *C. miniata* in spite of the fact that they refuse to accord fully

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with the hypothetical type. For example, our nos. 2131 and 2132, growing together in "placer wash," agree in having a large intricately branched root, from the crown of which the stems spring. Both have corollas with the galea yellowish-green, scarcely as long as the tube, but our field notes read as follows: "2031, bracts most remarkably bright red; 2132, bracts a splendid golden yellow with orange tips." No one studying these two critically can fail to decide they are the same species, and can scarcely fail to refer them to *C. miniata*.

Castilleja Bennittii, n. sp.—Very short-lived perennial, sparsely hirsute throughout with a short dense cinereous subscabrous indument underneath: stems few, simple or often branched, 2–3 dm. high: leaves linear, entire or irregularly lobed, the lobes narrower than the blade: inflorescence dense, becoming more open and slender in age, old rose in color: bracts three-cleft, the lobes blunt, the middle the largest: calyx 15–20 mm. long, the subequal clefts only about 5 mm. deep, these divisions shallow-lobed, the short rounded lobes terminating the prominent ciliate calyx nerves: corolla slightly, sometimes scarcely, exserted, 15–22 mm. long; the galea about half as long as the tube, the short rounded teeth hardly differentiated in the strongly nerved saccate lower lip.

There seems to be no near relative to which to ally this species, unique in its color and floral parts. It was pronounced new in 1911 on the strength of specimens submitted by DORMAN BENNITT of Twin Falls. It is a pleasure to dedicate it to its discoverer, who accompanied the collectors on part of the 1912 trip and assiduously assisted in the field work. The type is no. 1714 secured on the sagebrush plains of Shoshone and Twin Falls, June 24, 1912.

CASTILLEJA RHEXIFOLIA **pubens,** n. var.—The branches of the caudex and the stem-bases scaly: stems numerous (usually several of them short and sterile), with a villous crisped pubescence quite to their bases: lower leaves also with a similar, though shorter pubescence.

No. 2023, on stony brush slopes, from Jarbidge, Nevada, July 11, 1912, is taken as the type.

Castilleja curticalix, n. sp.—Plants harsh to the touch, often decidedly so, in rather small clumps, from short-lived perennial roots: stems few–many, 2–4 dm. high, simple or nearly so, softly cinereous-hirsute near the base, becoming glabrate upward: leaves

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numerous, scarcely smaller above, often rather closely ascending, scabrous on both sides, sometimes ciliate on the margins, linear to narrowly lanceolate, 2–6 cm. long, usually entire, but not rarely with one pair of widely divaricate lobes: bracts resembling the leaves: the moderately crowded inflorescence at length rather open, predominating color yellow or greenish-yellow, but often flushed with red: calyx 1.5 cm. long, scarcely exceeding the corolla tube, subequally cleft above and below, the primary divisions cleft at apex into long acute teeth: corolla 2–2.5 cm. long, galea 7–10 mm. long, the lower lip scarcely saccate, with very short teeth, the outer the longer.

Apparently the nearest allies of the proposed species are *C. fasciculata* A. Nels. and *C. lutescens* (Greenm.) Rydb. It differs from both in the very short calyx, also from the former in the harsh pubescence (in which it resembles *C. lutescens*), and from the latter in the narrower leaves. No. 2099 from Gold Creek, Nevada, July 24, 1912, is taken as the type. No. 2098 from the same locality and 1983 from Jarbidge, July 8, are both fairly representative. It occurs mostly on grassy slopes.

CASTILLEJA FASCICULATA **inverta,** n. var.—Much resembling the species, but pubescence merely a fine puberulence: calyx exceeding the corolla, more deeply cleft above than below, its lobes short-bifid: galea and lip subequal.

Practically all the perennial species formerly referred to *Orthocarpus* have been transferred to *Castilleja*, even when the corolla lips are subequal. This seems advisable, the more so in the present instance, because of its evident affinity with *C. fasciculata* A. Nels. In the subequal lips of the corolla, which is surpassed by the calyx, the proposed variety is strongly differentiated, and if subsequent collections show the characters given above to be constant it will become *C. inverta*.

Secured at Rattlesnake Springs, Idaho, on hard gravelly soil among the sagebrush, no. 1915, July 4, 1912.

Pentstemon rex, n. sp.—Having the pubescence, herbage, and aspect of *P. perpulcher* A. Nels., BOT. GAZ. **52**:273. 1911.—Corolla bright blue, about 3.5 cm. long, rather abruptly ampliate above the tube proper, wholly glabrous without and within as are also the anthers: sterile filament slightly dilated, glabrous or sparsely hispid-pubescent with short unequal hairs: anther cells dehiscent from the base upward for about three-fourths their length, leaving a closed saccate apical portion.

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This could be referred to *P. perpulcher* were it not for the strong contrast between its rather small flowers and the large showy ones of this. Then the dehiscence character is unique in the *P. glaber* group. Some of the red-flowered species of *Pentstemon*, recently erected into a separate genus by Dr. GREENE, have anthers in which the upper portion of the cells remain closed and saccate, but none are known to the writers in the other sections of the genus. The SACCANTHERA section, of course, has anthers in which the base of the cell is the part that remains closed.

The following four numbers are all representative, but the first is named as the type: no. 1999, Jarbidge, Nevada, July 9, 1912; no. 977, MACBRIDE, Twilight Gulch, Owyhee Co., Idaho, June 23, 1910 (distributed as *P. speciosus* Dougl.); 1774, House Creek, Owyhee Co., Idaho, June 29, 1912; 2157, Bieroth's Ranch (McDonald Creek), Nevada, August 2, 1912.

PENTSTEMON PERPULCHER **pandus**, n. var.—Smaller than the species, the leaves more or less curved or arcuate: puberulence very dense, that of the stem extending to the rachis but not to the pedicels and calyx.

No. 1884, July 2, 1912, on the high plains, near the "Hot Hole" of the East Bruneau is the type.

Downingia brachyantha (Rydb.), n. comb.—*Bolelia brachyantha* Rydb., Mem. N.Y. Bot. Gard. **1**:458. 1900.

Downingia corymbosa (A. DC.), n. comb.—*Clintonia corymbosa* A. DC. Prodr. **7**:347. 1838.

Because of some splendid specimens secured of these species in the field work of 1912, our attention has been called to the fact that in accordance with the action of the Vienna Congress ("*nomina conservanda*") these species must be transferred.

Erigeron elkoensis, n. sp.—Plant low, subcinereous with a rather dense short more or less retrose pubescence throughout, with a short simple or sparingly branched caudex clothed with dead leaf-bases: stems few, simple, decumbent-ascending, monocephalous, leafy throughout or often naked-pedunculate above, about 4–10 cm. long: leaves numerous on the crowns, 2–4 cm. long including the petiole, oblong-spatulate, subacute, tapering to a narrowly winged petiole as long as or longer than the blade, inclined to be conduplicate; stem leaves similar, becoming smaller upward and linear: heads large, 20–25 mm. broad: bracts lance-linear, acute, unequal, one-nerved, in 2–3 series, the inner scarious-margined,

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entire or fimbriate, granular-glandular, the outer green, hirsute as well as glandular: rays 15–20, conspicuously purple, rather broad, 3-toothed at apex: disk flowers yellow: achenes (young) pubescent.

In habit this suggests *E. leiomeris* Gray, but in other respects is very different. No. 2068, secured on open pebbly slopes, near Pole Creek in the Burnt Timber Mountains, Elko Co., Nevada, is the type.

ERIGERON POLIOSPERMUS **latus**, n. var.—Rougher pubescent than in the typical form, the crowns of the caudex clothed with dead leaf-bases: leaves unusually broad (3–4 mm.): heads large, very broad (the disk about 15 mm.) and the rays rather long and broad: involucre sparsely hispid, with the tips of the bracts granular-glandular, otherwise nearly or quite naked: rays purplish to white: achenes brown, glabrate.

This was a most striking plant on the black volcanic sands on which it was secured. In habit and aspect it suggested the *E. compositus* group rather than its real affinity, and led to its being tentatively designated as a species, *E. latus*. The technical characters, however, scarcely warrant such a disposition. Three Creek, Owyhee Co., Idaho, no. 1861, July 1, 1912.

ROCKY MOUNTAIN HERBARIUM
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SIR JOSEPH DALTON HOOKER

F. O. BOWER

[In a memorial oration delivered at the University of Glasgow, June 25, 1912, Professor BOWER spoke of Sir JOSEPH D. HOOKER as a traveler, a geographer, a geologist, a morphologist, an administrator, a scientific systematist, and a philosophical biologist. There is danger that HOOKER's great contributions to taxonomy will overshadow, for the biologists of a later generation, his important relation to the development of evolutionary theory. With the permission of Professor BOWER, therefore, that part of his oration dealing with HOOKER as a philosophical botanist is here reproduced.—EDITOR.]

I hope I have not wearied you with these brief sketches of four of the great systematic works of Sir JOSEPH HOOKER. I have gone somewhat more into detail than is quite justified in a public speech. But this has been done with a definite end in view. It was to show you how fully he was imbued with the old systematic methods; how he advanced, improved, and extended them, and was in his time their chief exponent. His father had held a similar position in the generation before him. But the elder HOOKER, true to his generation, treated his species as fixed and immutable. He did not generalize from them. His end was attained by their accurate recognition, delineation, description, and classification. The younger HOOKER, while in this work he was not a whit behind the best of his predecessors, saw further than they. He was not satisfied with the mere record of species as they were. He sought to penetrate the mystery of the origin of species. In fact, he was not merely a scientific systematist in the older sense. He was a philosophical biologist in the new and nascent sense of the middle period of the nineteenth century. He was an almost life-long friend of CHARLES DARWIN. He was the first confidant of his species theory, and, excepting WALLACE, its first whole-hearted adherent. But he was also DARWIN's constant and welcome adviser and critic. Well indeed was it for the successful launch of evolutionary theory that old-fashioned systematists took it in hand. Both DARWIN and HOOKER had wide and detailed knowledge of species as the starting-point of their induction.

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Before we trace the part which HOOKER himself played in the drama of evolutionary theory, it will be well to glance at his personal relations with DARWIN himself. It has been seen how he read the proof-sheets of the *Voyage of the Beagle* while still in his last year of medical study. But before he started for the Antarctic he was introduced to its author. It was in Trafalgar Square, and the interview was brief but cordial. On returning from the Antarctic, correspondence was opened in 1843. In January 1844 HOOKER received the memorable letter confiding to him the germ of the theory of descent. DARWIN wrote thus: "At last gleams of light have come, and I am almost convinced that species are not (it is like confessing a murder) immutable: I think I have found (here's presumption!) the simple way by which species become exquisitely adapted to various ends." This was probably the first communication by DARWIN of his species theory to any scientific colleague.

The correspondence thus happily initiated between DARWIN and HOOKER is preserved in the *Life and letters of Charles Darwin*, and in the two volumes of *Letters* subsequently published. They show, on the one hand, the rapid growth of a deep friendship between these two potent minds, which ended only beside the grave of DARWIN in Westminster Abbey. But what is more important is that these letters reveal, in a way that none of the published work of either could have done, the steps in the growth of the great generalization. We read of the doubts of one or the other; the gradual accumulation of material facts; the criticisms and amendments in face of new evidence; and the slow progress from tentative hypothesis to assured belief. We ourselves have grown up since the clash of opinion for and against the mutability of species died down. It is hard for us to understand the strength of the feelings aroused, the bitterness of the attack by the opponents of the theory, and the fortitude demanded from its adherents. It is best to obtain evidence on such matters at first hand, and this is what is supplied by the correspondence between DARWIN and HOOKER.

How complete the understanding between the friends soon became is shown by the provisions made by DARWIN for the publication of his manuscripts in case of sudden death. He wrote in August 1854 the definite direction "HOOKER by far the best man

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to edit my species volume," and this notwithstanding that he writes to him as a "stern and awful judge and sceptic." But again, in a letter a few months later, he says to him "I forgot at the moment that you are the one living soul from whom I have constantly received sympathy." I have already said that HOOKER was not only DARWIN'S first confidant, but also the first to accept his theory of mutability of species. But even he did not fully assent to it till after its first publication. The latter point comes out clearly from the letters. In January 1859, six months after the reading of their joint communications to the Linnaean Society, DARWIN writes to WALLACE "You ask about LYELL'S frame of mind. I think he is somewhat staggered, but does not give in. . . . . I think he will end by being perverted. Dr. HOOKER has become almost as heterodox as you or I, and I look at HOOKER as by far the most capable judge in Europe." In September 1859 DARWIN writes to W. D. FOX "LYELL has read about half of the volume in clean sheets. . . . . He is wavering so much about the immutability of species that I expect he will come round. HOOKER has come round, and will publish his belief soon." In the following month, writing to HOOKER, DARWIN says: "I have spoken of you here as a convert made by me: but I know well how much larger the share has been of your own self-thought." A letter to WALLACE of November 1859 bears this postscript: "I think that I told you before that HOOKER is a complete convert. If I can convert HUXLEY I shall be content." And lastly, in a letter to W. B. CARPENTER, of the same month, DARWIN says: "As yet I know only one believer, but I look at him as of the greatest authority, viz. HOOKER." These quotations clearly show that, while LYELL wavered, and HUXLEY had not yet come in, HOOKER was a complete adherent in 1859 to the doctrine of the mutability of species. Excepting WALLACE, he was the first, in fact, of the great group that stood round DARWIN, as he was the last of them to survive.

The story of the joint communication of DARWIN and of WALLACE to the Linnaean Society "On the tendency of species to form varieties, and on the perpetuation of varieties and species by natural means of selection" will be fresh in the minds of you all, for the fiftieth anniversary of the event was lately celebrated

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in London. It was Sir CHARLES LYELL and Sir JOSEPH HOOKER who jointly, and with the author's permission, communicated the two papers to the society, together with the evidence of the priority of DARWIN in the inquiry. Nothing could then have been more apposite than the personal history which Sir JOSEPH gave at the DARWIN-WALLACE celebration, held by the Linnaean Society in 1908. He then told, at first hand, the exact circumstances under which the joint papers were produced. Nor could the expressions used by the President when thanking Sir JOSEPH, and presenting to him the DARWIN-WALLACE Medal, have been improved. He said: "The incalculable benefit that your constant friendship, advice, and alliance were to Mr. DARWIN himself, is summed up in his own words, used in 1864: 'You have represented for many years the whole great public to me.'" The President then added: "Of all men living it is to you more than to any other that the great generalization of DARWIN and WALLACE owes its triumph."

Having thus sketched the intimate relations which subsisted between HOOKER and DARWIN, it remains to appraise his own positive contributions to philosophical biology. He himself, in his address as President of the British Association at Norwich in 1868, gives an insight into his early attitude in the inquiry into biological questions. "Having myself," he says, "been a student of moral philosophy in a northern university, I entered on my scientific career full of hopes that metaphysics would prove a useful mentor, if not a guide in science. I soon found, however, that it availed me nothing, and I long ago arrived at the conclusion so well put by AGASSIZ, when he says 'We trust that the time is not distant when it will be universally understood that the battle of the evidences will have to be fought on the field of physical science, and not on that of the metaphysical.'" This was the difficult lesson of the period when evolution was born. HOOKER learned the lesson early. He cleared his mental outlook from all preconceptions, and worked down to the bed-rock of objective fact. Thus he was free to use his vast and detailed knowledge in advancing, along the lines of induction alone, toward sound generalizations. These had their very close relation to questions of the mutability of species. The subject was approached by him through the study

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of geographical distribution, in which, as we have seen, he had at an early age become the leading authority.

The fame of Sir JOSEPH HOOKER as a philosophical biologist rests upon a masterly series of essays and addresses. The chief of these were the introductory essay to the *Flora Tasmaniae*, dealing with the antarctic flora as a whole; the essay on the distribution of arctic plants, published in 1862; the discourse on insular floras in 1866; The Presidential address to the British Association at Norwich in 1868; his address at York, in 1881, on geographical distribution; and finally, the essay on the vegetation of India, published in 1904. None of these were mere inspirations of the moment. They were the outcome of arduous journeys to observe and collect, and subsequently of careful analysis of the specimens and of the facts. The dates of publication bear this out. The essay on the antarctic flora appeared about twenty years after the completion of the voyage. The essay on the vegetation of India was not published till more than half a century after HOOKER first set foot in India. It is upon such foundations that HOOKER's reputation as a great constructive thinker is securely based.

The first-named of these essays will probably be estimated as the most notable of them all in the history of science. It was completed in November 1859, barely a year after the joint communications of DARWIN and WALLACE to the Linnaean Society, and before the *Origin of species* had appeared. It was to this essay that DARWIN referred when he wrote that "HOOKER has come round, and will publish his belief soon." But this publication of his belief was not merely an echo of assent to DARWIN's own opinions. It was a reasoned statement, advanced upon the basis of his "own self-thought," and his own wide systematic and geographical experience. From these sources he drew for himself support for the "hypothesis that species are derivative and mutable." He points out how the natural history of Australia seemed specially suited to test such a theory, on account of the comparative uniformity of the physical features being accompanied by a great variety in its flora, and the peculiarity of both its fauna and flora as compared with other countries. After the test had been made, on the basis of the study of some 8,000 species, their characters, their spread,

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and their relations to those of other lands, he concludes decisively in favor of mutability and a doctrine of progression.

How highly this essay was esteemed by his contemporaries is shown by the expressions of LYELL and of DARWIN. The former writes "I have just finished the reading of your splendid essay on the origin of species, as illustrated by your wide botanical experience, and think it goes far to raise the variety-making hypothesis to the rank of a theory, as accounting for the manner in which new species enter the world." DARWIN wrote "I have finished your essay. To my judgment it is by far the grandest and most interesting essay on subjects of the nature discussed I have ever read."

But besides its historical interest in relation to the species question, the essay contained what was, up to its time, the most scientific treatment of a large area from the point of view of the plant-geographer. He found that the antarctic, like the arctic flora, is very uniform round the globe. The same species in many cases occur on every island, though thousands of miles of ocean may intervene. Many of these species reappear on the mountains of Southern Chile, Australia, Tasmania, and New Zealand. The southern temperate floras, on the other hand, of South America, South Africa, Australia, and New Zealand, differ more among themselves than do the floras of Europe, Northern Asia, and North America. To explain these facts he suggested the probable former existence, during a warmer period than the present, of a center of creation of new species in the Southern Ocean, in the form of either a continent or an archipelago, from which the antarctic flora radiated. This hypothesis has since been held open to doubt. But the fact that it was suggested shows the broad view which he was prepared to take of the problem before him. His method was essentially that which is now styled "ecological." Many hold this to be a new phase of botanical inquiry, introduced by Professor WARMING in 1895. No one will deny the value of the increased precision which he then brought into such studies. But in point of fact it was ecology on the grand scale that Sir JOSEPH HOOKER practiced in the Antarctic in 1840. Moreover, it was pursued, not in regions of old civilization, but in lands where nature held her sway untouched by the hand of man.

This essay on the flora of the Antarctic was the prototype of

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the great series. Sir JOSEPH examined the arctic flora from similar points of view. He explained the circumpolar uniformity which it shows, and the prevalence of Scandinavian types, together with the peculiarly limited nature of the flora of the southward peninsular of Greenland. He extended his inquiries to oceanic islands. He pointed out that the conditions which dictated circumpolar distribution are absent from them, but that other conditions exist in them which account for the strange features which their vegetation shows. He extended the application of such methods to the Himalaya and to Central Asia. He joined with ASA GRAY in like inquiries in North America. The latter had already given a scientific explanation of the surprising fact that the plants of the eastern states resemble more nearly those of China than do those of the Pacific slope. In resolving these and other problems, it was not only the vegetation itself that was studied. The changes of climate in geological time, and of the earth's crust as demonstrated by geologists, formed part of the basis on which he worked. For it is facts such as these which have determined the migration of floras. And migration, as well as mutability of species, entered into most of his speculations. The essays of this magnificent series are like pictures painted with a full brush. The boldness and mastery which they show sprang from long discipline and wide experience.

Finally, the chief results of the phytogeographical work of himself and of others were summed up in the great address on "Geographical distribution" at York. The Jubilee of the British Association was held there in 1881. It had been decided that each section should be presided over by a past President of the Association, and he had occupied that position at Norwich in 1868. Accordingly at York, HOOKER was appointed President of the Geographical Section, and he chose as the subject of his address "The geographical distribution of organic beings." To him it illustrated "the interdependence of those sciences which the geographer should study." It is not enough merely to observe the topography of organisms, but their hypsometrical distribution must also be noted. Further, the changes of area and of altitude in exposed land surfaces of which geology gives evidence, are

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essential features in the problem, together with the changes of climate, such as have determined the advance and retrocession of glacial conditions. Having noted these factors, he continued thus: "With the establishment of the doctrine of orderly evolution of species under known laws, I close this list of those recognized principles of the science of geographical distribution, which must guide all who enter upon its pursuit. As HUMBOLDT was its founder, and FORBES its reformer, so we must regard DARWIN as its latest and greatest lawgiver." Now, after thirty years, may we not add to these words of his, that HOOKER was himself its greatest exponent?

You will have felt how tenuous is the line of limitation, if line indeed there be, between morphological reality and morphological abstraction; between the unit observed, and the summation of such units into a progression; between the static and the dynamic study of living things. It was this line that was crossed by DARWIN; and, as I have shown, HOOKER was the first of his friends to follow. To the general public he was perhaps the least known of the great triumvirate of Glasgow. The results he achieved do not touch everyday life so nearly as those of KELVIN or of LISTER. This is perhaps natural, for while he was the leading botanist of his time, he was, before all, a philosopher. In him we see the foremost student of the broader aspects of plant life at the time when evolutionary belief was nascent. His influence at that stirring period, though quiet, was far-reaching and deep. His work was both critical and constructive. His wide knowledge, his keen insight, his fearless judgment were invaluable in advancing that intellectual revolution which found its pivot in the mutability of species. The share he took in promoting it was second only to that of his life-long friend, CHARLES DARWIN.

UNIVERSITY OF GLASGOW

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THE LICHENS OF MT. ROSE, NEVADA

ALBERT W. C. T. HERRE

Mt. Rose, with an altitude of 10,800 ft., is the highest peak in the region about Lake Tahoe, and lies about 15 miles southwest of Reno, Nev. A forest of *Pinus ponderosa* extends from the base of the peak at an approximate elevation of 6000 ft. to perhaps 8000 ft. The higher elevations on to the timber line, which is at an altitude of about 10,000 ft., are covered more or less by *Tsuga mertensiana*, *Libocedrus decurrens*, and *Pinus monticola*. During the Comstock boom this timber was greatly depleted, parts being deforested even up to the timber line. Along the water courses are scattered *Salix* sp., *Amelanchier* sp., and various smaller shrubs. Above 8000 ft. a large part of the mountain, in common with all the ranges about, is bare of trees and strewn with bowlders or plentifully sprinkled with dikes and outcrops of rock.

The remarkably original and valuable observations of Dr. J. E. CHURCH, of the University of Nevada, have furnished us with our knowledge of the climatology of Mt. Rose. For a number of years he has maintained on this isolated and well-nigh inaccessible peak a meteorological station unique in America. For a large part of the year snow lies upon the upper part of the peak, while at no time of the year is it entirely absent except where the winds keep the rock ledges swept bare. Snow may fall in quantity at any time of the year, though in late summer it nearly disappears, and when fresh-fallen lies but a short time. In the forested portion of the higher altitudes the snow forms great mounds which act as storage tanks, supplying water gradually to the lower levels. The summit temperatures are not excessively low, though of course cold weather prevails much of the time; $-10°$ F. is the lowest recorded, but freezing weather occurs at any time of the year.

The most noticeable features of the lichen flora of the mountain are, so far as my observations extend, the utter absence of bark-dwelling species or those of dead or decorticated wood, and the equally conspicuous absence of earth lichens.

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In part, at least, the absence of corticolous lichens is due directly to the winds of enormous velocity which are prevalent in this region. Gales of 50 miles an hour are frequent, while at times the inordinate velocity of 150 to 170 miles an hour is reached. As these winds sweep the mountain slopes, they carry sand or dust, sleet, and fine hard snow; the abrasive action of this flying material affects the bark of the conifers upon which it impinges in such a way that they appear as if freshly sandpapered. I was unable to find any indication of either lichens or mosses upon the bark of any tree or shrub examined.

The dearth of earth lichens may be in part explained by other causes, such as excessive dryness, the erosive action of floods caused by the rapid melting of snow when the Chinook winds blow in early spring, etc. But as yet I cannot understand the failure to find any trace of such genera as *Cladonia*, *Stereocaulon*, *Solorina*, *Cetraria*, and similar genera containing species characteristic of alpine situations. Perhaps prolonged search in early summer just after the disappearance of the greater part of the snow would reveal some of them.

The conditions noted above offer no hindrance to the growth of rock lichens. In the wooded slopes lichens occur on all rocks, but not abundantly, even where not shaded by the pines. But at 8000 ft. one comes suddenly into a region where lichens are both extraordinarily numerous and remarkably conspicuous. From here to the summit the dominant species is *Gyrophora reticulata*, which is excessively abundant; but the great bowlders strewing the mountain side and obstructing the trail are also spotted and blotched with huge, brilliant masses of *Acarospora chlorophana*, while *Caloplaca elegans* lends a gleam of fire to the somber landscape. The number of species occurring from here to the summit is very small, but this is amply compensated for by the number of individuals found in what one may term the *Gyrophora reticulata* formation. The species collected were as follows:

1. *Staurothele umbrina* (Ach.) Tuck.—Forming dark stains on rocks along the summit.

2. *Lecidea atrobrunnea* (Ram.) Schaer.—Abundant on all kinds of rocks at 8000 ft. and above; exceedingly variable, and perhaps

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I have included more than one species, but as the more aberrant forms do not have fertile asci I cannot place them elsewhere. Varying in color from a clear saddle brown to black-brown. Much infested by a parasitic fungus which causes black, morbid, apothecia-like growths.

3. *Lecidea plana* Lahm.—Identification doubtful, but agrees in all essentials.

4. *Gyrophora rugifera* (Nyl.) Th. Fr.—Abundant on the south side of ledges at 10,800 ft. and for several hundred feet below; not found on the north side of the mountain. Growth luxuriant, but very rarely fertile.

5. *Gyrophora reticulata* (Schaer.) Th. Fr.—Excessively abundant from 8000 ft. upward. Occurring in all kinds of situations and forming the dominant lichen. Rather variable, but all forms may be referred to this species, whether typically foliose or reduced to a dense, uniform, crustaceous rock covering. According to the investigations of Dr. R. HEBER HOWE, who has recently examined the lichen types of the Linnaean Herbarium, *Lichen deustus* of LINNAEUS is really *G. reticulata*, which therefore becomes a synonym of *G. deustus* (Lin.) R. H. Howe.

6. *Acarospora chlorophana* (Wahlb.) Mass.

7. *Acarospora cervina* (Pers.) Koerber.

8. **Acarospora thermophila** Herre, n. sp.—Thallus somewhat orbiculate to effuse, areolate and fissured, of small lobulate squamules which are more or less stalked or stipitate beneath, the clustered stalks often branched, their height reaching 7 mm. Surface of squamules imbricate-lobate, the lobes very small, except marginally where they may be slightly expanded. Upper surface a pale yellow-brown or clay-brown; beneath black. No reactions visible.

Apothecia rare, small to medium, solitary or several grouped together, their surface more or less roughened and wrinkled, or sometimes fissured; an evident narrow thalline margin present; epithecium yellow-brown; hypothecium yellowish or very pale brownish; thecium colorless, turning to very deep blue with I; paraphyses simple, not septate, subcoherent, slender, their tips not enlarged; asci broadly clavate or top-shaped, measuring 24.8–

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30.5 μ in breadth by 61–68 μ in length; spores colorless, exceedingly numerous, short ellipsoid to subglobose, 1–2 μ broad by 2–4.5 μ long.

Common on rocks everywhere in the desert about Reno, Nev., at an altitude of 4700 to 6000 ft.; not rare on Mt. Rose at 8000 ft. and above, and abundant in the Sierras along the Truckee River near the Nevada-California state line at an altitude of 6000 ft.

In a preceding paper (BOT. GAZ. **51**:286–297. 1911) this plant was mistakenly called by me *Acarospora thamnina*. It is certainly the most successful xerophyte of the Nevada desert, growing in the driest places, where it is exposed to the most intense light and heat. The apothecia are rarely developed, but the scales are commonly covered with a parasitic fungus so that they appear fertile, but their true condition is readily shown by careful sectioning.

9. **Acarospora thamnina** (Tuck.) Herre.—*Leconora thamnina* Tuck., Genera Lichenum, 120. 1872; *L. cervina* b. *thamnina* Tuck., Synopsis **1**:202. 1882.—Thallus of small, dense irregular clumps 8–15 or rarely 25 mm. or more in diameter, with domelike or irregularly rounded surface, or more or less flattened. On closer examination the surface is seen to be made up of a great number of small to minute, closely appressed, and highly irregular, plicate, or even imbricate, lobulate squamules; these are continued downward into stems which coalesce to form finally flattened, rootlike stipes, the whole clump with its basal stipe reaching a height of 10–15 mm. in well grown specimens. Color various shades of brown; often gray or bluish-gray pruinose; usually more or less blackened by a parasitic fungus; the under surface dead black. No reactions observable.

Apothecia rare, small or minute, 0.2–0.8 mm. in diameter, rarely more than one in squamule, immersed, their surface more or less roughened or gyrose; thalline margin entire, rather thick; much darker in color than the thallus; epithecium yellow; hypothecium pale; paraphyses simple, straight, their tips not enlarged, oleoguttate, 1–2.7 μ broad; asci cylindrical, 13–18 μ broad by 48–55 μ long; when treated with I the colorless thecium is first blue, then wine-red, and finally tawny; spores short ellipsoid to ellipsoid, 0.75–1.25 μ broad by 3.3–4.5 μ long.

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A rare plant, known only from the cold high Sierras. Collected by BOLANDER at Mono Pass in 1867, and so far as I know not reported authentically by others. Occurring on earth deep in the crevices of rocks beside the observatory on the summit of Mt. Rose, associated with *Gyrophora rugifera*. For the determination of this singular *Acarospora* I am indebted to Dr. W. G. FARLOW, who kindly compared my material with that in the Tuckerman Herbarium.

10. *Lecanora rubina* (Vill.) Ach.

11. *Lecanora melanophthalma* (DC.) Jatta.

12. *Candelariella cerinella* (Flk.) A. Zahlbr.—On rocks at 10,800 ft. and also on the thallus of other lichens.

13. *Blastenia ferruginea* (Huds.) Arn.—On the thallus of other lichens and also on rocks at 10,800 ft.

14. *Caloplaca elegans* (Link) Th. Fr.—Common at all elevations from 8000 ft. to the summit.

15. *Caloplaca murorum* (Hoffm.) Th. Fr.—Not very abundant at 8000 ft.

16. *Xanthoria lychnea laciniosa* (Schaer.).—On the thallus of *Gyrophora rugifera* and in crevices of rocks at 10,800 ft.; not very plentiful.

17. *Physcia tribacia* (Ach.) Tuck.—A few small, sterile specimens were collected at 8000 ft. and at 10,800 ft.

EVERSON, WASH.

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BRIEFER ARTICLES

A NEW WOOD-DESTROYING FUNGUS

(WITH SIX FIGURES)

A very interesting polypore was sent to Professor ATKINSON at the botanical laboratory of Cornell University during the winter of 1912–13. The plant, collected by Dr. F. A. WOLF at the Alabama Polytechnic Institute, was found growing on some of the woodwork in the engineering building, where it was apparently causing considerable damage. A stairway and floor situated near water pipes were so badly rotted that it was necessary to replace them, and the wainscoting under the steps was entirely covered with a layer of mycelium, which was at first yellow and later dark brown. An examination showed that the mycelium was growing through the wood and also over the exposed surfaces, where it produced a soft papery layer of pale umbrinous color which could be easily separated from the substratum. In manner of growth and the appearance of the mycelium, the plant resembles *Merulius lacrymans*, but instead of the hymenophore being composed of the vermiform, anastomosing folds of that genus, a stratum of dark fuligineous pores was formed (figs. 1–3). The tubes were very fragile and friable when dry, the condition in which the fungus was found. A microscopic examination showed that the color of the tubes was almost entirely due to the very numerous dark brown spores which filled the pores and were often massed on the surrounding mycelium. The trama of the pores and the subiculum on which they were formed were composed of pale umbrinous hyphae (figs. 4, 5).

The wood on which the fungus was growing was in advanced stages of decay, of a dark brown color and checked into small cubes. Much of it could be crumbled between the fingers, and when sections were cut the spring wood separated from the summer wood. A part of the wood was bald cypress (*Taxodium distichum*) and a part long leaf pine (*Pinus palustris*). Strange to say, in the cypress the late or summer wood, which is more resinous, was more badly decayed than the spring wood, which in some places remained quite firm. The reverse was true in the pine; the spring wood in some instances was reduced almost to a powder, while the summer wood remained intact. All attempts to germinate the spores or to get a culture from the mycelium in the wood failed, so that no work with pure cultures, to find the action of the fungus on the wood or to determine with certainty that it was responsible for the decay present, was possible.

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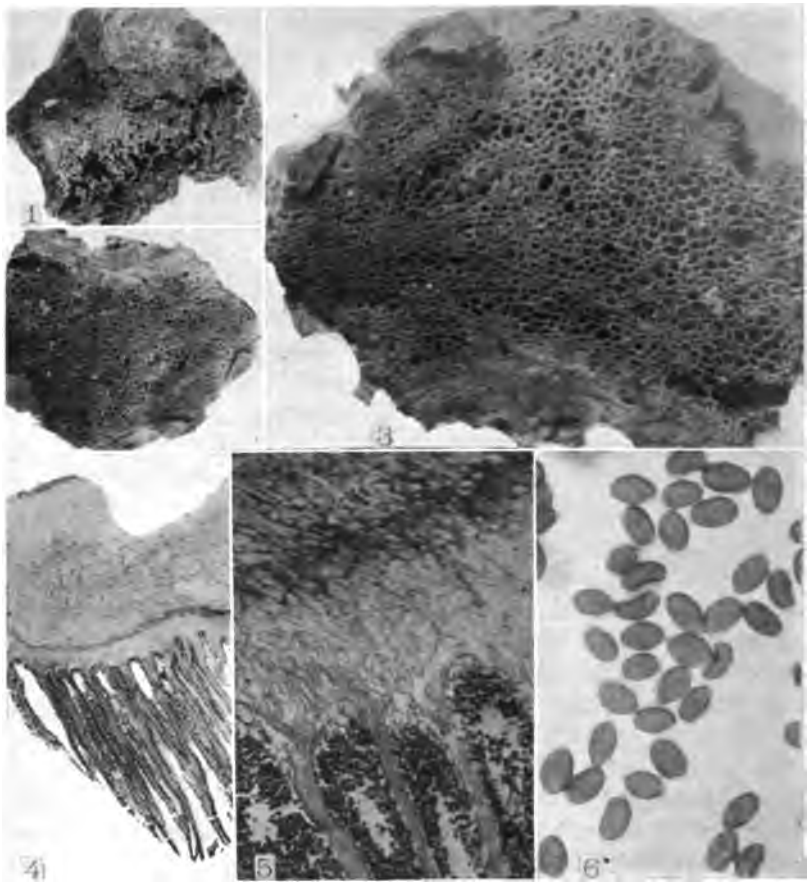
This plant seems to occupy a position in the Polyporeae similar to that of *Merulius lacrymans* and related species in the Meruliae and to *Coniophora* among the Thelephoraceae. It has the same dark dusty



FIGS. 1–6.—*Poria atrosporia:* figs. 1, 2, portions of fruiting surface, nat. size; fig. 3, same, ×2; fig. 4, photomicrograph of section through pores, ×10; fig. 5, same. ×76; fig. 6, photomicrograph of spores.

spore mass and the light colored mycelium forming thin sheets over the substratum. The spores of *Coniophora cerebella* and *Merulius lacrymans* are slightly different in color, being more brown than fuligineous, and those of *Coniophora cerebella* larger than the spores of this species, but they are of the same shape (fig. 6).

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Search through the literature of described species revealed no plant of like character. It is therefore described as a new species, and provisionally placed in the genus *Poria*, although it is recognized that the plants of this genus are a heterogeneous group which sooner or later will be separated into several genera or distributed among the genera of pileate forms with which they correspond in texture and other characters. The specific name *atrosporia* is given because of the abundance of dark spores. A technical description is as follows:

Poria atrosporia, n. sp.—Mycelium within the substratum or in a superficial layer of soft cottony or thin papery consistency; color pale umbrinous: sporophore resupinate, broadly effused, easily separable: margin sterile, pale umbrinous: hymenophore porose, not stratose, very fragile and friable when dry; pores 1–5 mm. deep, dissepiments thin, mouths irregular to subrotund, 1–5 to a mm.: trama pale umbrinous, but pores deep fuligineous because of the abundance of dark spores; spores oval, dark brown, $4–5.5 \times 8–10 \mu$; cystidia none. Habitat, structural timber of coniferous wood.

Mycelio substratum penetrante vel stratum superficium byssinum vel papyraceum formante; sporophora resupinata, late effusa, a matrice separabilis; margine sterili, umbrino-pallido; poris non stratosis, siccatis fragilis et friabilis, 1–5 mm. longis; parietibus tenuibus; ore irregulari vel subcirculari, 1–5 quoque mm.: trama umbrina-pallida sed poris fuligineis ob copiosos umbrinos; sporis ovatis $4–5.5 \times 8–10 \mu$; cystidiis nullis. Hab. ad ligna fabricata coniferarum.—ADELINE AMES, *Cornell University, Ithaca, N.Y.*

A SAFETY RAZOR MODIFIED FOR CUTTING HAND-SECTIONS

(WITH ONE FIGURE)

Since the advent of the many styles of "safety razors," biologists have looked with covetous eye upon their keen and cheap blades, seemingly unadapted to any purpose except that intended by the manufacturer. Microtomists have produced several devices to utilize these keen edges and at the same time hold the blades solidly so as to avoid trembling, but, so far as I am aware, none of these razors has been used for hand-sectioning, or, if the blades have been used, the handles have been of no assistance.

Some time ago, needing section razors for the use of large classes, I looked over the various kinds of safety razors for sale in shops and found among them one known as the "Durham-Duplex," which, by slight modification, has become very well adapted to the purposes for which

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students have need of a section cutter. This razor has two advantages over most safety razors, so far as our present purposes are concerned. In the first place, it is much like an old-style razor in general shape, the blade, however, being removable and protected by a nickel-plated brass guard. In the second place, the blades are thicker, longer, and stiffer than those provided with most safety razors.

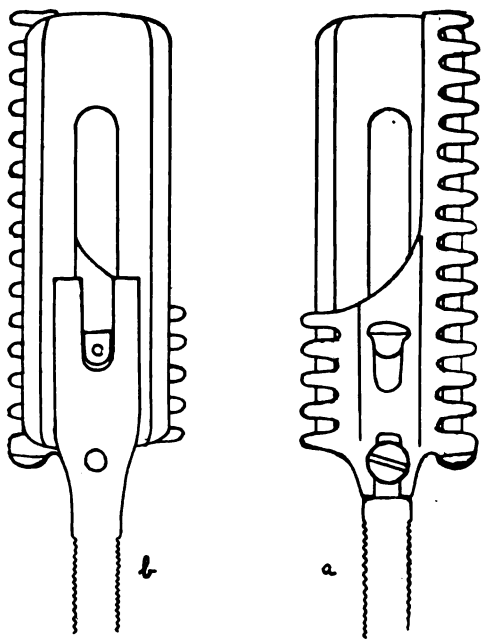

FIG. 1.—Modified safety razor: explained in text

The accompanying drawings (fig. 1) will show at a glance the changes that have been made upon the "Durham-Demonstrator." As shown by *a*, the protecting shield has been cut away so as to leave a portion of the blade exposed for use. The other drawing (*b*), showing the other side of the razor, illustrates the cutting off of the brass supporting handle, thus leaving the blade free beneath. A screw fitted into the handle at the base of the blade is at once the means of holding the latter rigid, as well as of permitting its easy removal for cleaning or changing the cutting edge, the slot filed into the base of the guard making of this a very simple operation.

In practice this razor has proved very successful with large classes, providing an abundance of sharp edges as well as saving the time of an assistant on whom the work of honing would otherwise fall.—J. P. GIVLER, *Southwestern College, Winfield, Kansas.*

ON STEMONITIS NIGRESCENS AND RELATED FORMS

That MACBRIDE, in his *North American slime-moulds*, retains *Stemonitis nigrescens* Rex as a distinct and well marked species, while the LISTERS, in their *Monograph of the Mycetozoa*, refer it unhesitatingly

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and with only the briefest comment to *S. fusca*, seems to warrant some further elucidation. Judging by the type specimen only, a portion of which was sent to me some years ago by the late Dr. REX, one would be justified in according to his species at least varietal rank. The strikingly dark color, the stiff, upright habit of the sporangia, not curved or drooping even at the edges of the clusters, and their small size (stalk less than 1 mm., total height 4.5 mm. or less) are features which appear to render this form recognizable at sight. Moreover, many gatherings made during the past ten years in as widely separated localities as New England and Colorado show that this dark, dwarf form is fairly common in the United States. It should be noted also that with the distinct external features noted above certain microscopic features are usually associated, such as a more or less imperfect development of the surface net, the meshes of which show spinelike processes, and reticulated spores of a smoky-brown color.

A number of gatherings made in Colorado, however, throw light on the variable character of *S. nigrescens*. Seven such gatherings are before me. They all agree in the short-stalked, upright, dwarf habit, and in the reticulated spores. But the color of the clusters of sporangia varies markedly from dull ferruginous to almost black; the surface net in one of the specimens is as perfectly developed and as free from spinous processes as in any typical specimen of *S. fusca;* while the spores vary in color from pale to dark smoky-brown, the former showing a very faint and delicate reticulation which is much more pronounced in the case of the darker-spored specimens. I cannot but conclude that these are all forms of one and the same species, and that they should be regarded as a dwarf variety of *Stemonitis fusca* Roth.

This opinion is strengthened by the examination of a specimen collected at Pagosa Springs, Colorado, in August 1911. It shows the same dense clusters of stiff, upright, dark smoky-brown sporangia, short-stalked, and measuring less than 4 mm. in height. The small-meshed surface net shows a few small spines. The spores, 8.9 μ in diameter, are rather dark in color, but instead of being reticulated they are closely and minutely spinulose. In my opinion this is a dwarf form of *Stemonitis herbatica* Peck, and bears the same relationship precisely to that species as do the dwarf forms commented on above to *S. fusca*. I conclude, therefore, that the LISTERS were correct in merging *S. nigrescens* Rex with *S. fusca* Roth, but that the former constitutes a well marked variety, though ill-defined by the designation *nigrescens*.—W. C. STURGIS, *Colorado Springs, Colorado.*

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CURRENT LITERATURE

BOOK REVIEWS

Physiological plant anatomy

The appearance of a fourth edition of HABERLANDT's well known work,[1] almost exactly 25 years after the first edition was published, is an indication of the importance of the book and the service it has rendered to the physiological aspect of plant anatomy. The previous edition, reviewed in this journal,[2] has been completely revised, and the changes, although limited in extent, serve to incorporate the results of more recent investigation. The number of pages has been increased from 616 to 650, and the illustrations from 264 to 291.

Among the additions are sections entitled "Einrichtungen für besondere mechanische Leistungen," which include the discussion of various hairs and hooks functioning as supports of climbing plants; and "Speichergewebe für Atmungsstoffe" and "Speichergewebe für ökologische Zwecke," dealing with certain aspects of the storage tissues of plants, but presenting little new data.

The most important changes appear in the twelfth chapter, entitled "Die Sinnesorgane," which has been entirely rewritten, with the inclusion of much new material. Foremost among the new data are the results of the author's studies on the structure for light perception in leaves. They include the various lens cells or ocelli, as well as various cells below smooth outer surfaces. Several papers presenting these data have already been noted in these pages.[3] Both in this chapter and elsewhere in the volume the author maintains his well known teleological interpretation of the date in spite of the opposite trend of modern investigation. Fortunately this does not detract from the importance of his experiments or the accuracy of his data.—GEO. D. FULLER.

MINOR NOTICES

Key to trees.—The authors[4] of a *Key to New England trees* have again given us a convenient and reliable pocket manual pertaining to our native

[1] HABERLANDT, G., Physiologische Pflanzenanatomie. Vierte, Neubearbeitete, und vermehrte Auflage. Imp. 8vo. xviii+650. *figs. 291*. Leipzig: Wilhelm Engelmann. 1909. *M* 19.

[2] BOT. GAZ. **38**:146–148. 1904.

[3] COLLINS, J. FRANKLIN, and PRESTON, HOWARD W., Illustrated key to the wild and commonly cultivated trees of the northeastern United States and adjacent Canada. Small 8vo. pp. vii+184. *figs. 279*. New York: Henry Holt & Co. 1912. $1.35 in cloth, $2.50 in leather.

[4] BOT. GAZ. **42**:399. 1906, and BOT. GAZ. **48**:472–474. 1909.

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trees and those common in cultivation in the northeastern United States and adjacent Canada. The book is free from unnecessary technical terms and descriptive details which are essential to a comprehensive flora, so that the volume can be used easily and intelligently by the layman as well as profitably by the scientifically trained individual. Identification of a given tree is made by a simple key, based on leaf characters, leading directly to the species, which is illustrated by an outline drawing of a typical leaf associated usually with a reproduced photograph in halftone of the bark. Each tree is given its scientific name, as well as the common name by which it is known. The drawings are all made in actual proportions, the natural size being shown graphically by a line-scale accompanying each figure. We need more such books to encourage and popularize careful field observation.—J. M. GREENMAN.

Officinal plants and drugs.—MITLACHER[5] has brought together in convenient compilation the plants recognized in all of the approved pharmacopoeias, 22 in number. The nomenclature is that of the Vienna Congress, and the sequence is that of WETTSTEIN'S *Handbuch*. The data given are as follows: geographical distribution and culture of medicinal plants, the vegetation form, the drugs obtained, those drugs regarded as especially strong and those recognized as "officinal" in different countries, etc. It is interesting to note the distribution of these 638 officinal plants, representing 125 families. Of the cryptogams, only 23 such plants are used (Phaeophyceae 2, Rhodophyceae 7, Fungi 7, Pteridophytes 7), representing 16 families; while the gymnosperms add only 21 conifers. The 594 officinal plants among angiosperms, representing 107 families, are distributed as follows: Archichlamydeae 323, Sympetalae 197, and Monocotyledons 74.—J. M. C.

Illinois Academy of Science.—The volume of transactions of the fifth annual meeting (February 1912) of the Illinois Academy of Science has just appeared. A symposium on conservation includes "Conservation of our forests," by HENRY C. COWLES, and "Conservation ideals in the improvement of plants," by H. J. WEBBER. In addition to these papers, the following of botanical interest were presented: "Notes on the forests of Ogle County, Ill.," by W. L. EIKENBERRY; "Competition and general relationships among the subterranean organs of marsh plants," by EARL E. SHERFF; "The range of evaporation and soil moisture in the oak-hickory forest association of Illinois," by WADE MCNUTT and GEO. D. FULLER; and "Germination and growth of the cottonwood upon the sand dunes of Lake Michigan, near Chicago," by GEO. D. FULLER.—J. M. C.

Volvox.—An extended discussion of *Volvox*, based upon living and fixed material mounted whole in glycerin jelly, is presented in a pamphlet by JANET.[6]

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[5] MITLACHER, WILHELM, Die offizinellen Pflanzen und Drogen. pp. viii+13. Wien: Carle Fromme. 1912. *M* 6.25.

[6] JANET, CHARLES, Le *Volvox*. 8vo. pp. 151. *figs. 15*. Limoges: Ducourtieux et Goût. 1912.

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The colony is compared with the blastula stage of animal embryology, and has a pore like the blastopore. The antheridium develops in the blastula fashion with a "phialopore," as does also the new colony, whether formed asexually or from the egg. The figures are very diagrammatic, but interesting and probably accurate. No nuclear detail is attempted. The most striking feature of the paper is the terminology. Every structure has a technical name, even when ordinary literary French would serve as well.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS

Inheritance in maize.—COLLINS[7] has made some interesting observations on the progeny of an all-white ear of maize that appeared suddenly in a field planted with a variety known as Gorham yellow dent. Since the character with which he was dealing develops in the endosperm and usually shows complete dominance in crosses, this variation is out of the ordinary. The author classes it as a case of mutative reversal of dominance. To the reviewer such a view respecting the phenomenon seems unwise. In the descendants of the seeds of this ear, yellow was dominant to lack of yellow in varying degrees; it only remains then to explain the non-development of yellow in the original aberrant ear. It has been generally accepted that dominance or lack of dominance is only another way of describing the somatic appearance of a heterozygote. It has nothing to do with segregation and is valuable simply as an indication of zygotic composition. The true classification of any individual can be determined only by breeding from it, for there are characters so variable in their dominance that the appearance of the heterozygote may be similar to either homozygote (*AA* or *aa*). In spite of its variability, however, dominance does not just happen. It has its causes. An individual *AA* may be crossed with various kinds of *aa* individuals and the degree of dominance be different in each cross, but these various manifestations are due to internal differences between the *aa* organisms. On the other hand, external conditions may affect the manifestation of a character either when in a heterozygous or when in a homozygous condition. One may assume, therefore, that dominance is not a phenomenon of great variability when both external and internal conditions of development are identical. For these reasons, the reviewer has a suspicion that COLLINS' mutative reversal of dominance was nothing but suppressed development due to some abnormal environmental condition, possibly the accidental presence of some particular metallic salt in the spot of soil in which the plant grew. The reviewer has observed somewhat similar phenomena, but has never thought his own ignorance of their exact cause a sufficient excuse for an attack on well established theories.

Seeds from COLLINS' "albinistic" ear were planted and the progeny investigated. His results show clearly that he was dealing with the behavior of two

[7] COLLINS, G. N., Heredity of a maize variation. Bur. Pl. Ind. Bull. 272. pp. 23. *pl. 1. fig. 1.* 1913.

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factors for yellow endosperm, Y_1 and Y_2, of which one is much more effective in producing the yellow pigment than the other. Such an assumption he regards as "violent," it being just as violent as have been the assumptions of all Mendelian experimentalists who have made mathematical interpretations of breeding facts. The author is also greatly disturbed over the question of whether or not the segregation ratios that he obtained fit the theory of error. It seems to the reviewer, however, that considering the possibility of experimental error in work with maize, he is to be congratulated on having done some very careful work to have them fit "theory" as well as they do.

Notwithstanding the fact that the results obtained agree well with the assumption of two yellow factors that are given above, with only a few minor variations of classification due to the difficulty of distinguishing light yellows from white, the author concludes "that while the segregation is usually numerically exact, it is by no means complete; that is, the dominant character is not completely absent from individuals of the recessive class." "This," he says, "is shown not only by the presence of a faint yellow color in most of the seeds, but also by the fact that apparently pure white seeds from an ear in which the classes were well marked may produce seed with a fully developed yellow color when self-pollinated." Consequently he favors the idea of gametic impurity in the sense that extracted dominants and recessives may transmit traces of the alternative character.

Again this conclusion seems opposed to the facts submitted. If one has a set of light yellow and white seeds in an apparent ratio of 3:1, he makes his classification as best he may by somatic appearance. He then grows the whole series and finds out *what the true classification of the parents was*. This the reviewer has done on similar material, with the result that the ratio of the mother seeds *proved* to be 3:1; this the author either has not done or has not reported. If then the *white ears* obtained do not again breed true, one might have the right to assume gametic contamination; but the author reports no such evidence. As a matter of fact, extracted recessives and extracted dominants do appear to throw the alternative character on rare occasions, but the phenomenon is so rare that one may better assume that a germinal rearrangement (mutation) has occurred. Of course in any species some variations are more likely to occur than others, which may be taken as evidence of a kind of latency. But this is only the kind of latency that is analogous to the tendency of a chlorine atom to split off from a complex benzene derivative, rather than one of the more conservative radicals such as methyl. It is evidence that certain rearrangements in a particular germ plasm are more likely to occur than others.—E. M. East.

Studies of Nicotiana hybrids.—In two papers, appearing almost simultaneously, Goodspeed[8] has reported the results of his investigations on

[8] Goodspeed, T. H., Quantitative studies of inheritance in *Nicotiana* hybrids. Univ. Calif. Publ. **5**: no. 2. pp. 87–168. *pls. 29–34*. 1912; *ibid*. no. 3. pp. 169–188. 1913.

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possible correlations between seed characters and plant characters, and on the inheritance of certain quantitative character complexes in crosses between various *Nicotiana* species and varieties.

In that part of the contribution concerned with somatic correlations the author deals with a cross between the varieties *virginica* and *macrophylla* of the species *Nicotiana tabacum*. F_1 seeds were divided arbitrarily into the classes light, medium, and heavy. The light and medium seeds germinated more quickly than the heavy seeds, and plants resulting from the former matured more quickly than those from the latter. It does not appear, however, that the general belief that heavy seed gives more vigorous plants than light seed is incorrect. Moreover, the total germination of heavy seed was higher than that of the other two classes.

The author continually speaks of the dominance of one plant over another, a mediaeval mode of expression that makes it impossible to draw any conclusions from his observations on his F_1 generation. Likewise he finds that the heavy seed gave, in F_2, 39 per cent of "dominants" (resembling *macrophylla*), 52 per cent of intermediates, and 9 per cent of "recessives" (resembling *virginica*); while the light seed gave 18 per cent dominants, 49 per cent of intermediates, and 33 per cent of recessives. With such a method of describing results it is not surprising that he invents a theory for their interpretation that will no doubt be very interesting to cytologists, for in it he assumes that the "tube nucleus" of the pollen grain unites with the fusion "endosperm" nucleus of the embryo sac. He assumes that there are two "determiners," one functioning to produce *virginica* characters and the other *macrophylla* characters. The generative nucleus, he says, may bear either, and the "tube nucleus" may bear either. The same alternatives are assumed for the egg nucleus and the fusion "endosperm" nucleus. Then, simply by having a *macrophylla* generative nucleus unite with a *macrophylla* egg nucleus, and a *macrophylla* "tube nucleus" unite with a *macrophylla* fusion nucleus, he gets a heavy seed having *macrophylla* characters. *Quod erat demonstrandum*. Charitably granting that the words "tube nucleus" were slips of the pen, there is no excuse for founding a theory that the two male nuclei carry different "determiners" upon unsupported data of this character.

In the second part of his work, the author has studied the degree of dominance and the variation in size of corolla diameter in the parents and F_1 generation of crosses between varieties of *Nicotiana acuminata*. The corolla breadth of the F_1 generation was found to be the arithmetical mean of the two parents. The fluctuation in corolla breadth, both in individual plants and in the population as a whole, was greater in F_1 than in the parents. These conclusions, at least as to the degree of variability of the F_1 generation, are at variance with the results of several careful investigators (the reviewer can count twelve such offhand), but it is impossible to criticize GOODSPEED's data, for he does not give them in the form of frequency distributions. He simply reports maximum and minimum measurements, which may or may not mean anything.

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He does indeed give two plates of frequency polygons, but his distributions are for number of flowers measured on particular dates, with no statement as to their size, and for relative frequency of flowers of certain sizes, with no data on the actual number of flowers measured or the number of plants upon which they were borne. Apparently the parents upon which data were taken were too few to warrant such sweeping conclusions.

In the second paper, also, one gathers that the F_2 generation there reported on is more variable than the F_1 generation; but no data are recorded. This paper purports only to be a note, however, and one may expect some data of greater consequence when the really large amount of work that the writer has done is reported in full.—E. M. EAST.

Knot disease of citrus trees.—HEDGES and TENNY[9] give a complete account of a knot disease of citrus trees that had been briefly described in a preliminary account by Miss HEDGES.[10] The disease has been found on lime trees in Jamaica and in one instance in Florida. It manifests itself by woody knots or swellings which appear on the branches and trunks of the diseased trees. The knots are usually round or somewhat elongated in the direction of the axis of the branch which bears them. They attain a diameter of 2–3 inches, and by their growth usually girdle the branch upon which they are seated, this causing the death of all the parts of the branch above the knot. Groups of fascicled branches, forming witches-brooms, often grow out from the knots, but these branches also are short-lived. The knots consist mostly of woody tissue, at first covered by bark which soon dies and crumbles away. All the tissues of the knots, as well as the tissues of the branches near the knots, are found to be infected with the brown mycelium of a fungus which was described by Miss HEDGES as *Sphaeropsis tumefaciens*. The mycelium of this parasite has been observed to spread to a distance of 45 cm., and it seems probable that it can spread to greater distances. Secondary knots are produced by the mycelium which spreads through the branches. The growth of the fungus on a large number of media, its characteristics, and numerous infection experiments are described at length by the authors.—H. HASSELBRING.

The cause of leaf asymmetry.—BOSHART, working in GOEBEL'S laboratory, reports the results of certain observations and experiments on asymmetry and anisophylly.[11] He concludes that the size of any given leaf part is determined by the area it occupies in the vegetative point. Further development

[9] HEDGES, F., and TENNY, L. S., A knot of citrus trees caused by *Sphaeropsis tumefaciens*. Bur. Pl. Ind. Bull. 247. pp. 9–74. *pls. 10. figs. 8.* 1912.

[10] HEDGES, FLORENCE, *Sphaeropsis tumefaciens*, nov. sp., the cause of the lime and orange knot. Phytopath. 1:63–65. *pl. 1.* 1911.

[11] BOSHART, K., Beiträge zur Kenntnis der Blattasymmetrie und Exotrophie. Flora 103:91–124. 1911.

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depends on nutrition, a poor food supply causing but slight enlargement of the part, whereas a good food supply causes considerable enlargement. The vegetative point, on the other hand, is unrelated to nutrition, so far as its symmetry is concerned. Contrary to most previous investigators, BOSHART finds no evidence that gravity or light influences leaf symmetry. It is believed rather that both anisophylly and leaf asymmetry are merely an expression of the symmetry of the plant as a whole. For example, anisophylly, and in most instances asymmetry also, is associated with dorsiventrality, radial shoots being characterized commonly by isophylly and symmetry. It seems very doubtful if this radical view, giving little or no place to the operation of external factors, will displace the many experimental contributions of past years. Even in this contribution it is admitted that good nutrition can result in the development of the vegetative point of a dorsiventral shoot into a radial shoot. It would seem, then, according to BOSHART, that external factors determine what sort of a shoot develops, but that the type of leaf is tied up inexorably with a particular kind of shoot.—HENRY C. COWLES.

Photometric leaves and shoots.—WIESNER in continuing his already very extensive studies upon the light relations of plants returns to the consideration of the orientation of leaves in response to the direction of incident light. Fixed and variable positions[12] are distinguished and examples of the latter, which he regards as the more perfect response, are multiplied, the legumes furnishing the major portion. More exact studies are made of leaves only apparently related to light and termed pseudophotometric,[13] in contrast to those actually orienting themselves in response to incident light, and emphasis is laid upon the part played by epinasty and geotropism acting before and simultaneously with phototropism. Most photometric leaves are found to be pseudophotometric in the earlier stages of their development.

Relations similar to those existing in leaves are shown to obtain for shoots.[14] All shoots with photometric leaves are shown to be themselves photometric, but the category also includes the shoots of such conifers as *Abies* and *Tsuga*, with leaves showing very slight responses to light. The effect of light of different intensities is to be seen in the shoots of *Taxus baccata*, being perpendicular, that is showing euphotometry, while with more intense light they become panphotometric. Some interesting cases of the photometry of anisophyllous shoots are also discussed.—GEO. D. FULLER.

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[12] WIESNER, J. v., Über fixe und variable Lichtlage der Blätter. Ber. Deutsch. Bot. Gesells. **29**:304–307. 1911.

[13] WIESNER, J. v., Über aphotometrische, photometrische, und pseudophotometrische Blätter. Ber. Deutsch. Bot. Gesells. **29**:355–361. 1911.

[14] WIESNER, J. v., Über die Photometrie von Laubsprossen und Laubsprossystemen. Flora **105**:127–143. 1913.

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TOXIC INORGANIC SALTS AND ACIDS AS AFFECTING PLANT GROWTH

(PRELIMINARY COMMUNICATION)

CHAS. B. LIPMAN AND FRANK H. WILSON

The economic and industrial phases of the smelter fume and smelter waste problem, especially as related to crop growing in the vicinity of smelters, have been accompanied by a revival of interest in the scientific aspects connected with the physiological effects of the metallic compounds of copper, lead, zinc, and others on plant growth. There have appeared in 1905, 1908, and 1910, respectively, Bulletins 89, 113, and 113 revised, of the Bureau of Chemistry of the United States Department of Agriculture, and all by J. K. HAYWOOD, dealing with the subject of smelter fumes and smelter wastes as related to plant and animal life. HAYWOOD points out in these not only the fact that smelter fumes (largely SO_2) are very toxic to trees and other plants in the country surrounding the smelters, but in the last two bulletins mentioned devotes some attention to the subject of copper compounds in smelter wastes as affecting the value of irrigation water and soils to be used for crop production. It was this latter fact, together with a desire on our part to obtain further information on the action of manganese in soils and its effects on plants, that led the authors to institute the preliminary experiments which are described below. Before reporting these, however, it is of interest to turn for a moment to a brief review of the results thus far obtained by plant

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physiologists and chemists bearing on the subject under consideration.

The extreme toxicity of copper to plants under certain conditions has been responsible, it would appear, for some assumptions on the part of investigators as to the similarity in the action of copper in solutions and in soils. Thus JOHNSON, in his now classic work *How crops grow*, evidently assumes from the results obtained in solutions that copper is poisonous to plants even in very small quantities. Likewise the work of HEALD[1] and HARTER[2] with plants grown in solutions shows copper to be extremely toxic to plants. The former found, for example, that 1 part of copper in 404,423 parts of water was deadly to the garden pea (*Pisum sativum*), and that maize (*Zea mays*) seedlings are killed by the presence of 1 part of copper in 808,846 parts of water. OSTERHOUT[3] showed how water obtained from copper stills was poisonous to certain of the lower plants when containing merely traces of copper, and HAYWOOD, in the work above mentioned, states that in preliminary work with plants in soils containing copper, the growth of wheat and rye is "interfered with by the presence of 2.1 parts of soluble copper per million parts of earth in one soil, and by 3.5 parts of soluble copper per million parts of earth in another soil."

Some striking results on the effects of copper on plant growth which date back much farther than the last discussed were those obtained at the New York[4] and the Iowa[5] Experiment stations. It is a curious coincidence that both of these investigations were reported in the same year (1892), and they were both the result of the fungicide investigations in which it appeared of interest to ascertain how the continued use of fungicides would affect the soil in its productive capacity. In the New York bulletin, Part I of which is devoted to the subject in question, we find that among peas, wheat, and tomatoes, which formed the test plants, a resistance was noted to as much as 2 per cent and 5 per cent of $CuSO_4$ of the

[1] BOT. GAZ. **22**:125. 1896.

[2] Bur. Pl. Ind., U.S. Dept. Agric. Bull. 79. p. 40.

[3] BOT. GAZ. **44**:272 (footnote). 1907.

[4] N.Y. Exp. Sta. Bull. 41. 1892.

[5] Iowa Exp. Sta. Bull. 16. 1892.

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dry weight of the soil, and while the soils free from copper gave much larger yields of fruit and vine than did those grown in soils containing copper, it is amazing to note such extreme resistance to large quantities of a poisonous compound on the part of plants as manifested by more or less growth. The author of the paper gives the results only as preliminary and promises a much more thorough review of the investigations later. Twenty years have passed since, however, and we are unable to find any further published data from the New York Experiment Station on that subject. One more note in the paper is of interest, and that is of a contemporary paper by HASELHOFF,[6] the conclusions of which are quoted, in which that author states among other things that soluble copper salts are injurious to plants, and that while concentrations up to 5 ppm. are harmless, the presence of 10 ppm. of copper in soil has a marked retarding action. In the Iowa bulletin by PAMMEL we find that copper solutions had a marked retarding effect on the root development of plants, and that no roots at all developed where the concentration of copper was large. It is unfortunate that PAMMEL does not make mention of the concentrations of copper existing in the various experimental plots in the greenhouse.

So far as the effect of zinc salts on plant growth is concerned, there is but meager information. We have, however, the recent investigations in Germany on the effect of the zinc in galvanized iron cylinders, used for vegetation experiments, on plant growth. From these it would appear that zinc may be distinctly toxic to plant growth.

Experiments with manganese, however, have been very numerous; but their results have been so conflicting as to make more experimental work very desirable. The reader is referred for a more complete bibliography on the effects of manganese in soils on plant growth to a recent publication by W. P. KELLEY.[7]

Along with the problems of smelter fumes and smelter wastes, has come the idea of the condensation of the sulphur dioxide and the manufacture of H_2SO_4. It has been calculated by COTTRELL and others, however, who have made a careful study of the problems,

[6] Landw. Jahrb. 21:263.

[7] Hawaii Exp. Sta. Bull. 26.

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that the amounts of H_2SO_4 thus produced would be so enormous as to make it useless, since the demand for the acid is as yet quite limited. It has been suggested, therefore, among many other proposed uses for it, that H_2SO_4 be used in small quantities in the irrigation water to act as a solvent for soil minerals. It was this idea which suggested the preliminary experiment described below, along with the others, on the effects of the metallic salts on plant growth.

Experiments

The soil employed in the experiments was a light sand with a good humus supply, and was constituted chemically as follows:

Insoluble residue	75.77 per cent	Mn_3O_4	0.01 per cent
Soluble silica	2.94	P_2O_5	0.26
Fe_2O_3	2.05	MgO	0.36
Al_2O_3	3.38	Na_2O	0.17
CaO	1.59	K_2O	0.45
SO_3	0.02	Humus	2.35

Large 8-inch flower pots were filled with 12 lbs. of soil and treated with varying amounts of the solution of the salt to be tested, each cc. representing a known weight of the salt. The concentrations employed are noted in the tables in parts per million of water free soil. The plants tested were the vetch (*Vicia sativa*) and the Little Club variety of wheat. Eight seeds, which were carefully selected, were planted in each pot, and after some growth was made were thinned to 4 plants per pot. The pots were carefully irrigated so as to give the soil an optimum moisture content but not allow any moisture to percolate from the soil, thus preventing loss of the salts tested. The plants were all grown under glass and appeared to make good vigorous growth from the start. The appearance of the aphis and other insects in large numbers undoubtedly had something to do with diminishing the total yield of dry matter, but not enough to affect the results seriously. The vetch was not allowed to mature, but had to be harvested about the same time that the wheat was cut, because the mildew had attacked the plants rather seriously. The wheat was mature, however, when harvested. In the case of the vetch, the weight of the tops, as well as that of the roots, is given, while in the case of the wheat, only the

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weight of the tops as dry matter is recorded. The following tables give all other explanatory data and results of the experiments, and a discussion follows each table.

TABLE I

EFFECTS OF $CuSO_4$ ON PLANTS

$CuSO_4$ ppm.	Dry weight of vetch		Dry weight of wheat
	Roots gm.	Tops gm.	Tops gm.
0	4.5	12.0	18.5
5	1.8	20.5	15.7
10	5.5	20.0	16.2
20	4.0	21.0	17.5
40	5.5	17.5	13.0
100	3.0	18.0	16.5
200	4.5	14.0	17.2
400	Det. lost	12.0	19.0
600	...	....	12.7
1000	1.5	13.0	9.7

To one accustomed to regard $CuSO_4$ as an extremely poisonous salt for plants, the data in table I offer a surprise. While it is true that in the case of the wheat no stimulation from $CuSO_4$ is evident, its toxic nature likewise cannot be said to manifest itself until a concentration of 1000 ppm. is reached, if then. The last phrase is used advisedly, since the plants in the 600 and 1000 ppm. concentrations of $CuSO_4$ were started three weeks later than the rest. Germination of the wheat seeds seemed to proceed with much greater rapidity in the higher concentrations, but the plants though growing fast did not seem to possess the deep green color which is so characteristic of plants well nourished. These plants, however, matured at about the same time as the other wheat plants growing in the lower concentrations of $CuSO_4$, and produced normal heads.

In the case of the vetch plants, there seems to have been a stimulation due to $CuSO_4$, and then what might perhaps be looked upon as toxicity in the highest concentrations. It should be noted, however, that here, as in the case of the wheat, the vetch plants growing in the higher concentrations of copper were planted three weeks later than those growing in the soils with lower concentrations

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of copper. It is especially interesting here to mention the rapid and rank growth made by the vetch plants in the highest concentration of copper. All the seeds germinated and the vetch plants seemed to grow erect to a height of 6 inches or more before they began to bend downward by their own weight. The plants in the normal soil and in those with low concentrations of copper made but very little upright growth. One further point is of great interest in regard to the vetch plants, and that is that even at the highest concentrations of copper, the root development appeared to be normal and showed a marked and vigorous development of nodules (the soils were all inoculated). In general the effects of the copper sulphate as given in table I stand out in sharp contrast with the results above reviewed. They exhibit, on the one hand, a very much greater resistance to the effects of copper on the part of both wheat and the vetch plants than HAYWOOD observed in the case of wheat and rye as above noted; and on the other hand, our observations on the plants growing in the highest concentrations of copper given in table I lead us to believe that they will not withstand amounts of copper at all to be compared with those tolerated by the plants with which the experiments at the New York Experiment Station were carried out. From our results it would appear that the use of irrigation water containing a few parts of copper per million would not for many years react deleteriously to plant growth, while the very reverse is believed by HAYWOOD on the basis of his results. Further results were promised by HAYWOOD in 1908 based on his experiments with soils, but none have as yet appeared.

With reference to the cause of the injurious action of copper there are two explanations. One shows that there is direct injury due to absorption of copper as manifested by analysis, and frequently showing a large quantity of copper in plants sprayed with fungicides or in those growing in soils with a high copper content. HASELHOFF, however, whose work is cited above, claims that his investigations indicate an increased solution of lime and potash and subsequent leaching away of these materials through the action of copper sulphate, and that injury can be averted by applications of $CaCO_3$ to replace the losses taking place as indicated.

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The next series deals with the effects of $ZnSO_4$ on plants. The experiment was arranged similarly to the preceding, but the concentrations are slightly different, as shown in table II.

TABLE II

EFFECTS OF $ZnSO_4$ ON PLANTS

$ZnSO_4$ ppm.	Dry weight of vetch		Dry weight of wheat
	Roots gm.	Tops gm.	Tops gm.
0	4.5	12.0	18.5
10	1.5	12.5	17.5
20	3.0	20.0	18.5
100	4.5	22.0	18.5
200	4.5	20.0	14.6
300	2.0	20.0	10.8
400	1.8	18.0	19.8
500	1.5	15.5	13.7

These results do not show any marked toxicity of $ZnSO_4$ either for the vetch or the wheat. In the case of the vetch, there would even seem to be an appreciable degree of stimulation up to rather large concentrations of zinc. We can certainly not confirm any toxic effects of zinc salts on plants observed by others, at any rate so far as the concentrations employed above are concerned. The seeds germinated in the zinc-treated soils in a normal manner, and the plants in all the concentrations of the $ZnSO_4$ seemed to make a normal growth. Whatever differences may be noted in table II between the growths made in the pots of the different concentrations of salt employed must be attributed to insect or fungus injury rather than to any effect of the $ZnSO_4$. A comparison of our results with the effects of zinc noted by EHRENBERG, whose work is above cited, would seem to indicate that the later investigations[8] attribute both favorable and unfavorable effects to the zinc dissolved out from the galvanized iron cylinders used in the vegetation experiments. EHRENBERG claims that zinc acts favorably in that it displaces the bases from their insoluble combinations, and because of its harmful effect on soil organisms makes less competition for the plant in the latter's search for soil nitrogen. On the other hand, the same author points out that zinc sets free hydroxyl ions which exercise

[8] Landw. Versuchs. 72:15. 1910.

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a corrosive effect on plants, and that a too rapid displacement of bases in the soil and their subsequent leaching tends to cause soil acidity.

It is to be regretted that EHRENBERG's researches were carried out from the point of view merely of establishing the feasibility of employing vegetation cylinders containing zinc, and therefore we have nothing to guide us to the extent of the solution of zinc and the toxic limit thereof. It appears to us, further, that it is begging the question to assert that the toxic effect of zinc on soil organisms is of benefit to plants for the reason mentioned, because we have no definite data concerning the effects of zinc on soil bacteria or other soil organisms, and certainly not evidence enough, so far, to point to wide differences between the effects of zinc on the higher plants and soil bacteria. From the data in table II, at any rate, it would appear that plants will tolerate and will not be affected by even very considerable quantities of zinc.* In connection with this series of experiments in particular, it is desirable to have more experimental data, which we are attempting to secure in further experiments now under way.

The numerous and conflicting results obtained by different investigators in the study of the physiological effects of manganese salts on plants made it desirable to work further with these interesting compounds, and an experiment was arranged, therefore, in which this problem could be studied. The arrangement of the experiment with the results obtained are given in table III.

TABLE III

EFFECTS OF $MnSO_4$ ON PLANTS

$MnSO_4$ ppm.	Dry weight of vetch		Dry weight of wheat
	Roots gm.	Tops gm.	Tops gm.
0	4.5	12.0	18.5
20	4.0	9.5	16.2
40	3.5	11.5	20.0
80	6.0	15.0	21.5
200	4.0	18.0	25.1
400	5.0	17.5	23.2
800	5.5	19.5	26.0
2000	3.5	10.0	32.5

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It is clear from the data given in table III that both wheat and vetch are stimulated by the presence in the soil of $MnSO_4$ until the concentration of the latter there reaches an equivalent of 2000 ppm. for the wheat, and 800 ppm. for the vetch. Indeed, the total yields of dry matter obtained from the wheat growing in the pots with the highest concentrations of $MnSO_4$ surpass quite markedly the yields obtained in any of the pots of the other series described in this paper, and which were planted contemporaneously with the former. In the case of the vetch, the stimulation does not seem to be as great as in the case of the wheat, but from one series of experiments it is difficult to say if stimulation actually stops for the vetch at a concentration of 2000 ppm. of $MnSO_4$, since the poor growth obtained there may have been due to experimental error.

These results are an interesting contribution to the subject of the effects of manganese salts on plants. It is not our intention here to discuss the large number of investigations bearing on this subject, especially since this has already been so well done by KELLEY, in the work above referred to. In general, however, it would appear from such a review that the largest number of investigations on the subject indicate a stimulating power of manganese sulphate for plants, results with which ours are in accord. There are several cases, however, in which manganese compounds have been observed to depress crop yields, and this point would seem particularly to deserve brief discussion. The experiments dealing with this subject which have thus far been carried out have included tests of many different manganese compounds, and a comparison of the results obtained with different compounds in trying to determine the specific effects of manganese would seem to us to be manifestly unfair. One of us has pointed out elsewhere[9] that the anion as well as the kation of salts must be taken into consideration when the effects of salts on living organisms are studied. If such be the case, and we have every reason to believe that it is, then only the experiments bearing on the effects of $MnSO_4$ on plants should be compared when that subject is studied, and not the effects of the nitrate, chloride, oxide, sulphate, and other compounds. When that is done, it will be found that the percentage of investi-

[9] Centr. Bakt. 33:305.

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gations dealing with the subject under discussion in which $MnSO_4$ has not been found, in relatively small quantities, to act as a stimulant is indeed very small. Obviously when very large concentrations of $MnSO_4$ are employed it will be found toxic. As investigations of KELLEY above referred to have shown, a large variety of plants is affected more or less seriously by the manganese of soils which have shown a content of that material equivalent in some cases to more than 9 per cent of Mn_3O_4 in the soil. However, such manganiferous soils are limited in extent and, undoubtedly even then, owe their unfavorable nature, in part, to the form of the manganese which they contain. This point appears to us so important as to render a comparison of past results on manganese investigations of little value when it is not considered. It would seem from our results in this series of experiments, and others of a similar nature which they help to confirm, that distinct increases in crop yields of certain plants may be induced by employing $MnSO_4$ in small quantities as a soil amendment. The manganese content of most "normal"[10] soils is very small, and therefore the dangers arising from the presence of large amounts of manganese, as KELLEY has observed them on certain Hawaiian soils, are certainly very remote ones when considered in relation to these normal soils. Small additions of manganese should increase yields, therefore, without introducing dangers. We hope to report further results on this subject later.

As was pointed out above, it has been suggested by some chemists, among the many other uses proposed for H_2SO_4 when it is produced in enormous quantities from the SO_2 of the smelter fumes, that it could be employed in small quantities in the irrigation water, and, through the solution of mineral plant foods in the soil, be a considerable aid to the nutrition of plants directly, besides exerting perhaps a very marked influence indirectly on soil fertility as will be discussed later. In connection with soils containing black alkali, sulphuric acid would have an added value, if it were satisfactory in other ways, in that it would change the black to the white alkali more cheaply than gypsum does, and it could be applied more easily with irrigation water. Indeed, it is possible that in soils with a content of Na_2CO_3, not too large, the sulphuric

[10] Soils ordinarily cropped.

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acid treatment of soil may prove a valuable practice. The following experiment was considered, therefore, of very great interest as a preliminary test of the physiological effect of H_2SO_4 on plants, and its arrangement and results are set forth in table IV.

TABLE IV

EFFECTS OF H_2SO_4 ON PLANTS

H_2SO_4 ppm.	Dry weight of vetch		Dry weight of wheat
	Roots gm.	Tops gm.	Tops gm.
0	4.5	12.0	18.50
50	5.5	15.0	12.20
100	6.0	15.5	16.65
200	3.5	8.0	18.50
300	4.0	19.5	20.50
400	4.0	17.0	10.50
600	5.0	15.5	26.20

The foregoing data would seem to indicate that considerable amounts of H_2SO_4 may be added to soils without injury to plants. The objection, of course, to which such additions of acid would be open to in practice, is that when the lime and other bases have been neutralized in the soil by the acid, any further additions to the latter would tend to make an acid soil which is unfavorable for plant growth, but it is at any rate safe to assume that on strongly alkaline soils, where that condition is the interfering fact with plant growth, the acid treatment of soil should ameliorate its unfavorable condition to a marked degree. Moreover, we are not without a basis in fact for our assumption. SYMMONDS[11] has shown that when nitric acid to the extent of 600 pounds per acre was mixed with artesian water and applied to soils containing alkali, the yields of crops were greatly increased. It may be argued, of course, that this case is not an analogous one, since the nitric acid combines with bases in the soil to form nitrates which are an important food and even stimulant to plant growth, but it should also be remembered that, as one of us has already pointed out elsewhere, in a publication above cited, on the basis of direct investigations, that Na_2SO_4, produced through the action of H_2SO_4 on Na_2CO_3 (black alkali), is a stimulant to nitrification, and that thus an application of

[11] Agric. Gaz. N.S. Wales 21:257–266.

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H_2SO_4 to soils would render a service to the plant different in degree only but not in kind from that rendered by the application of HNO_3.

General remarks

While we offer the results given above as a preliminary report merely, on a series of investigations which we trust will ultimately make a thorough survey of the subject, we must conclude from these data that the tolerance of plants for certain of the inorganic salts, commonly regarded as very poisonous, is much greater than we have been wont to believe. It is true that we have commonly accepted the idea that very small quantities of poisons may act as stimulants, but our results show that plants do not merely tolerate but are actually stimulated by quite considerable quantities of these toxic salts. It is very desirable, therefore, to arrive at a definite understanding of the limits of toxicity of the substances in question, which we are now endeavoring to do.

It would appear to us, further, that the results we have obtained are sufficient evidence to prove that a more thorough investigation into the effects of smelter wastes on plants is necessary before we are enabled to determine justly whether from that standpoint smelter plants are inflicting appreciable injury on the soils immediately surrounding them and on the soils of contiguous territory.

Our results on the effects of $MnSO_4$ are considered of importance here both because of the stimulating effect of the former on plants and the attempts which have been made to make use of that fact in the employment of manganese salts as fertilizers. Moreover, our data form another link in the chain of evidence which show the stimulating effects of manganese sulphate on plants.

It may not be amiss to add here, also, that to make these investigations more complete we have been making studies of the bacterial flora in the soils employed in the experiments above described. From these we have already obtained data of great interest, which seem to indicate that the soil flora is permanently modified by the treatment of the soil outlined above. The publication of these results is reserved for another paper.

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THE TRANSPIRATION OF APPLE LEAVES INFECTED WITH GYMNOSPORANGIUM[1]

HOWARD S. REED AND J. S. COOLEY

(WITH ONE FIGURE)

The present paper reports the results of some studies upon the transpiration of apple leaves infected with the cedar rust fungus, *Gymnosporangium Juniperi-virginianae* Schw. Observation of trees attacked by this fungus shows that changes involving serious injury to the economy of the trees are produced. Such trees usually show characteristic dwarfing of both trunk and fruit.

The writers have undertaken to make some quantitative physiological studies upon these diseased trees as a part of a general pathological problem.

The study of the causative organism is highly important for plant pathology if any prophylactic measures are to be taken, but the reaction of the host is also a factor of importance if the action of the parasite is to be understood, or if efficient remedial measures are to be applied. The interest of the cultivator is principally in the host, but up to the present time that of the plant pathologist has been chiefly centered in the parasite. It is believed, however, that a physiological-pathological study of the host will yield results of no less interest than those of a strictly mycological nature.

A survey of the published work upon transpiration discloses few studies of the transpiration of diseased plants, although the assumption is frequently made that the rate of transpiration is affected by the presence of disease.

BLODGETT[2] has reported an observation upon the transpiration of excised branches of *Rubus* sp. infected with *Gymnoconia interstitialis*. In a given period (apparently shorter than 24 hours) the rusted branch absorbed 42 cc. of water, while a healthy branch possessing an equal number of leaves absorbed only 23 cc. of water

[1] Paper 24 from the Laboratory of Plant Pathology, Virginia Agricultural Experiment Station.

[2] BLODGETT, F. H., Transpiration of rust-infected *Rubus*. Torreya 1:32. 1901.

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under similar conditions. In spite of the greater amount of water absorbed, the rusted shoot was more or less flaccid, while the healthy shoot maintained a turgid condition. This behavior might be regarded as a consequence of the condition produced by the caeoma type of sorus produced by the fungus in question. The rupture of more or less extensive areas of the ventral epidermis of the leaf obviously facilitates the evaporation from the spongy parenchyma layers. Possibly other factors connected with the diseased condition may also operate to cause increased transpiration.

While not strictly parallel, it may be proper in this connection to cite results which BURGERSTEIN[3] obtained with the use of dilute solutions of camphor. He found that solutions containing about one part of camphor per thousand had an accelerating influence upon most plants investigated. Excised shoots, which were previously allowed to become somewhat wilted, revived more quickly when placed in camphor water than when placed in distilled water. By weighing the vessels of water in the two cases, it was shown that transpiration from the shoots went on more rapidly in camphor water than in distilled water. That camphor was absorbed by the excised shoots was shown by their pathological condition and death prior to the appearance of any such conditions in the parallel series in distilled water. It seems proper to regard this result as an example of transpiration under pathological conditions, since the deleterious substances thrown off by fungi may act similarly to the camphor.

Results of a somewhat similar import have been reported by one of the authors of this paper, showing that substances like tannic acid and pyrogallol when present in small amounts accelerate transpiration.[4] Small amounts of oxalic and acetic acids were likewise shown to accelerate transpiration. Since these substances are found as such in plants, it is possible that they may influence transpiration more or less independently of other factors.

The studies upon transpiration herein described were conducted

[3] BURGERSTEIN A., Über einige physiologische und pathologische Wirkungen des Kampfers auf die Pflanzen, inbesonders auf Laubesprosse. Verh. Kais. Kön. Zoolog.-Botan. Gesells. Wien 34:543. 1884.

[4] REED. H. S., The effect of certain chemical agents upon the transpiration and growth of wheat seedlings. BOT. GAZ. 49:81. 1910.

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upon the apple varieties York Imperial and Ben Davis in orchards near Middletown, Virginia, in 1911 and 1912. All of the trees upon which studies were made were more than eight years old, and, aside from a certain amount of dwarfing due to continued attacks of cedar rust in one of the orchards, the trees were in good physiological condition.

The time available for making satisfactory studies on transpiration of the diseased leaves was restricted to a period of about five weeks beginning near the middle of July. Before that date the cedar rust had not developed sufficiently to derange seriously, or at least uniformly, the activity of the apple leaves. Subsequent to this period, the fungus has injured or even killed more or less extensive areas in the infected leaves, and, in cases of severe infection, the leaves begin falling during the latter part of August.

The work here reported was carried out on leaves and twigs on the trees in their normal position. This method was believed to be preferable, since it has been shown by FREEMAN[5] that actively transpiring shoots do not usually transpire at a normal rate when removed from their own roots.

The data reported in the present paper were obtained by inclosing a few apple leaves in a glass cylinder and absorbing the exhaled water with weighed calcium chloride. The method of carrying on the experiments will be evident from the accompanying sketch of the apparatus (fig. 1), which is a type modified from that of FREEMAN (*loc. cit.*) and others.

In its essentials the apparatus consisted of three parts: a wide mouth glass jar (*A*) which contained the twig under experimentation, a calcium chloride tube (*B*), and an aspirator (*C*) which drew a known volume of air through the apparatus. The glass jar (*A*) was fitted with a soft rubber stopper which was cut through about three-fourths of its diameter. The opposing surfaces were notched at the center of the stopper to allow a twig to pass through, but the notch was small enough to insure a tight fit and prevent the passage of air. Two perforations in the stopper allowed glass tubes of 5 mm. diameter to pass. Tube 1, through which the air entered, extended to within 1 cm. of the bottom of the jar; tube 2,

[5] FREEMAN, G. F., A method for the quantitative determination of transpiration in plants. BOT. GAZ. 46:118. 1908.

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through which air left the jar, extended only about 1 cm. inside of the stopper. Tube 2 was connected with rubber tubing to a glass-stoppered calcium chloride tube (*B*). The calcium chloride tubes were accurately weighed at the laboratory before and after each experiment. The ground stoppers (*3*, *3*), when turned, effectually closed the tubes.

The aspirator for drawing air through the apparatus was a bottle of 19 liters capacity fitted with a siphon through which the flow

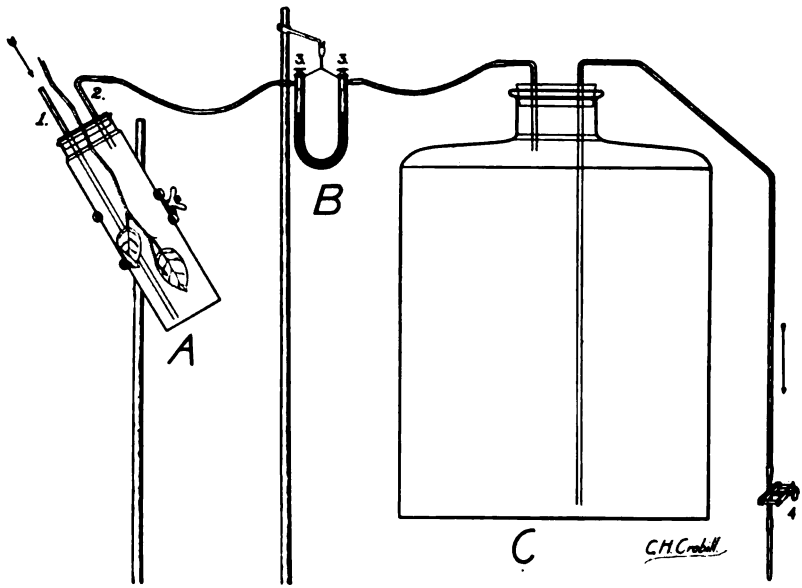

FIG. 1.—Apparatus for measuring transpiration: explained in text

could be regulated by means of a screw clamp (*4*). Three sets of apparatus were constructed and carried in a spring wagon which could be moved from tree to tree as occasion required.

The manner of conducting an experiment was as follows. The apparatus was placed at a tree where direct rays of sunlight would not strike it. A twig bearing leaves suitable for experiment was selected and inserted in the cleft rubber stopper, precautions against bruising or injuring the bark being used. In some cases one or two leaves had to be removed from the twig in order to make a good adjustment. After a few trials it was found that not more

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than two apple leaves could be used in an experiment with a moderate rate of aspiration; if more were used, water would sometimes collect in the jar *A*. A thermometer was inserted in the jar with the twig, or suspended close to it. The previously weighed U-tube was connected on one side with tube 2 and on the other with the aspirator *C*, which contained 19 liters of water. Care was taken that the temperature of the water used in the aspirator should be very close to that of the air. When the siphon was started, the stoppers (*3*, *3*) were turned to allow air to flow through the apparatus. The flow of water could be regulated by means of the screw clamp (*4*) after a little experience, so that the time required to draw out 19 liters should be close to an hour.

The first apparatus was set up with healthy leaves in the jar *A;* another experiment was similarly set up with leaves infected with cedar rust; a third experiment was set up but with the omission of the jar *A*. These three, each with its own aspirator, were started as nearly simultaneously as possible, and the temperature kept uniform. The purpose of the third set of apparatus was to determine the amount of moisture in 19 liters of air.

The criticism might justly be made that the evaporating power of the atmosphere was not taken into strict account by this sort of an experiment. If the purpose had been to study the conditions or amount of transpiration, such determinations should have been made, but the purpose was to study the comparative transpiration of the healthy and diseased apple leaves, and as such it is believed to fulfil its purpose. Another possibility of error might be found in the vapor pressure from the water in *C*, which would carry back some moisture into the tube *B* and cause the results to be too large. This source of error, however, is obviated by the use of the blank, whose increase in weight was subtracted from each of the accompanying tests.

As soon as the aspirator ceased running, the glass stoppers of the U-tubes were closed and the time noted. The leaves were plucked from the twig, placed in a labeled envelope, and taken to the laboratory along with the set of U-tubes. After weighing the tubes and computing the gain in weight, the necessary correction was made for the moisture absorbed from sources other than the leaves as registered by the increase in weight of the blank.

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The outline of the leaves used was carefully traced on paper and the area measured with a planimeter. The results thus obtained were computed and expressed as grams of water transpired per hour per sq. cm. A sample record sheet is herewith given, showing the records as made in the field.

TRANSPIRATION TEST NO. 2		TRANSPIRATION TEST NO. 3	
July 13, 1912		July 13, 1912	
Healthy York Imperial leaves		*Diseased York Imperial leaves*	
Temperature	30.5° C.	Temperature	30.0° C.
No. of leaves in test	1	No. of leaves in test	1
Area of leaves	21.3 sq. cm.	Area of leaves	35.2 sq. cm.
Vol. of air used	19 liters	Vol. of air used	19 liters
Exper't began	10:18 A.M.	Exper't began	10:14 A.M.
Exper't ended	11:20 A.M.	Exper't ended	11:16 A.M.
Duration	62 min.	Duration	62 min.
Final wt. of tube	91.555 gm.	Final wt. of tube	99.675 gm.
Initial wt. of tube	91.185 gm.	Initial wt. of tube	99.297 gm.
Difference	0.370 gm.	Difference	0.378 gm.
Water in equiv. vol. air	0.291 gm.	Water in equiv. vol. air	0.291 gm.
Water from leaves	0.079 gm.	Water from leaves	0.087 gm.
Water per hr. per sq. cm	0.0036 gm.	Water per hr. per sq. cm	0.0023 gm.

There were 52 determinations made upon healthy and diseased leaves of the York Imperial and 26 upon leaves of the Ben Davis. The results are presented in tabular form in tables I and II.

An inspection of the tables shows that the unit transpiration of the diseased leaves of both varieties of apples was in the majority of cases less than that of the healthy, although exceptions are to be noted. Some of these discrepancies may have arisen from unguarded errors of manipulation, but it is not probable that all are due to such cause.

It is not apparent that the ratio between the transpiration in the healthy and diseased leaves was subject to any regular hourly variation. The unit transpiration in each case naturally varied from hour to hour, but the ratios were in general the same at any given period of the day.

The average ratio of transpiration in the diseased and healthy

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TABLE I

TRANSPIRATION OF DISEASED AND HEALTHY YORK LEAVES

No.	Date	Hour at which experiment began	Transpiration of healthy leaves in gm. per hr. per sq. cm.	Transpiration of diseased leaves in gm. per hr. per sq. cm.	Percentage of water transpired by diseased leaves
	1912				
1	July 9	3:27 P.M.	0.00627	0.0064	103.6
2	9	4:15 P.M.	0.00257	0.00203	78.6
3	10	9:10 A.M.	0.0022	0.0033	150.0
4	10	10:20 A.M.	0.0074	0.0069	93.2
5	10	2:20 P.M.	0.0039	0.0043	110.3
6	10	3:50 P.M.	0.0041	0.0040	97.5
7	12	9:30 A.M.	0.0057	0.0065	114.0
8	12	10:45 A.M.	0.0134	0.0071	52.9
9	12	2:45 P.M.	0.0046	0.0048	104.3
10	12	4:05 P.M.	0.0079	0.0040	50.6
11	13	9:03 A.M.	0.0083	0.0106	127.7
12	13	10:14 A.M.	0.0036	0.0023	63.9
13	13	1:38 P.M.	0.00403	0.0043	106.7
14	15	9:06 A.M.	0.00508	0.0082	161.4
15	15	10:07 A.M.	0.0079	0.01033	130.7
16	16	10:20 A.M.	0.0257	0.0095	36.9
17	17	1:45 P.M.	0.0102	0.0078	76.4
18	17	3:00 P.M.	0.008	0.0022	31.4
19	17	8:17 A.M.	0.0102	0.0057	56.0
20	17	9:40 A.M.	0.143	0.0096	67.1
21	22	8:50 A.M.	0.0063	0.0028	44.4
22	22	9:50 A.M.	0.006	0.00505	84.2
23	22	1:50 P.M.	0.0101	0.00718	71.1
24	22	2:57 P.M.	0.0116	0.0088	75.1
25	23	8:38 A.M.	0.00505	0.0029	57.4
26	23	9:55 A.M.	0.00863	0.00573	66.4
27	23	2:45 P.M.	0.0104	0.00808	77.7
28	23	1:53 P.M.	0.0171	0.00589	34.4
29	25	2:35 P.M.	0.00617	0.00465	75.3
30	25	1:40 P.M.	0.0058	0.00425	73.3
31	26	9:30 A.M.	0.00908	0.0066	71.3
32	26	8:30 A.M.	0.0056	0.00439	78.4
33	26	1:35 P.M.	0.00737	0.006638	90.1
34	26	2:25 P.M.	0.00743	0.00408	54.9
35	27	9:25 A.M.	0.0105	0.0072	68.6
36	27	2:10 P.M.	0.0079	0.00606	76.7
37	Aug. 15	3:10 P.M.	0.0057	0.00335	58.8
38	15	4:30 P.M.	0.00445	0.0011	24.8
39	16	10:33 A.M.	0.00562	0.00375	66.7
40	16	2:45 P.M.	0.0055	0.0051	92.9
41	16	4:17 P.M.	0.0148	0.0107	72.3
42	17	9:40 A.M.	0.0047	0.00351	74.8
43	19	8:45 A.M.	0.00508	0.0025	49.2
44	19	3:20 P.M.	0.0055	0.0060	109.1
45	19	4:33 P.M.	0.0104	0.00706	67.9
46	20	10:54 A.M.	0.5003	0.0034	64.1
47	20	2:18 P.M.	0.002918	0.002908	99.6
48	20	3:35 P.M.	0.0036	0.00248	68.3

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TABLE I—*Continued*

No.	Date	Hour at which experiment began	Transpiration of healthy leaves in gm. per hr. per sq. cm.	Transpiration of diseased leaves in gm. per hr. per sq. cm.	Percentage of water transpired by diseased leaves
	1911				
49.....	July 26	4:00 P.M.	0.0025	0.0022	88.0
50.....	27	10:03 A.M.	0.0052	0.0043	82.7
51.....	27	2:14 P.M.	0.0024	0.0019	79.2
52.....	27	3:30 P.M.	0.0029	0.0016	62.1

TABLE II

TRANSPIRATION OF HEALTHY AND DISEASED BEN DAVIS LEAVES

No.	Date	Hour at which experiment began	Transpiration of healthy leaves in gm. per hr. per sq. cm.	Transpiration of diseased leaves in gm. per hr. per sq. cm.	Percentage of water transpired by diseased leaves
	1912				
60.....	July 11	9:40 A.M.	0.0101	0.009	89.1
61.....	11	10:27 A.M.	0.0101	0.0056	55.4
62.....	11	2:24 P.M.	0.0128	0.0073	57.0
63.....	11	3:40 P.M.	0.0094	0.0048	51.0
64.....	19	9:50 A.M.	0.0065	0.0032	49.2
65.....	19	8:40 A.M.	0.0032	0.0026	81.25
66.....	19	12:49 P.M.	0.0065	0.00305	46.9
67.....	19	1:50 P.M.	0.0043	0.00406	94.4
68.....	20	9:54 A.M.	0.0041	0.0025	61.0
69.....	20	8:45 A.M.	0.0042	0.0020	47.6
70.....	20	1:50 P.M.	0.0031	0.0037	119.3
71.....	29	2:20 P.M.	0.00675	0.00597	88.4
72.....	29	3:25 P.M.	0.00913	0.0066	72.5
73.....	30	9:20 A.M.	0.0053	0.0041	77.2
74.....	30	8:20 A.M.	0.00574	0.00409	71.2
75.....	30	2:44 P.M.	0.0100	0.00442	44.2
76.....	30	2:45 P.M.	0.0061	0.0045	73.8
77.....	Aug. 22	10:44 A.M.	0.0065	0.0045	69.2
78.....	22	3:08 P.M.	0.00638	0.0042	65.8
79.....	22	4:20 P.M.	0.0028	0.0034	121.4
80.....	23	9:28 A.M.	0.0044	0.0034	77.3
	1911				
81.....	July 22	3:45 P.M.	0.00243	0.0017	68.7
82.....	24	2:46 P.M.	0.0075	0.0039	52.0
83.....	24	2:57 P.M.	0.0067	0.0023	34.3
84.....	25	11:00 A.M.	0.0039	0.0061	156.4
85.....	25	3:45 P.M.	0.0079	0.0046	58.2

leaves comes out very nearly the same in each variety of apple studied, 78.3 for the York and 74.2 for the Ben Davis.

The ratios show certain differences if they are grouped according to periods covering different stages in the development of the disease. The first, from July 1 to 15, is a stage in which the fungus is still immature. At that time none of the peridia have broken

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open, although the thickened cushions are abundant. The second period, from July 17 to 31, marks a time in which the fungus has reached maturity and the leaf of the host begins to exhibit indications of serious injury. The diseased leaves at this time, owing to the expansion of the ventral surfaces by the cluster cups, are rolled toward the dorsal surface. During this second period many peridia open for the liberation of aecidiospores. The third period studied, August 15 to 23, covers a time in which the full effects of the fungus upon its host were very manifest. At that time many of the infected leaves had fallen from the trees, or, if they remained, they had a greater or less proportion of dead tissue. In table III the percentages of water transpired in these three periods are given.

TABLE III

TRANSPIRATION BY PERIODS

Percentage of water transpired by diseased leaves

Dates	York Imperial	Ben Davis
July 1–16	94.7	69.1
17–31	66.5	71.3
Aug. 15–23	70.7	83.4
For entire time of the experiments	78.3	72.4

From these figures it appears that in the first period the average unit transpiration of the diseased York leaves was nearly as great as that of the healthy leaves. In the second period the ratio dropped to 66.5, and rose to 70.7 in the third period. The ratios in the case of the Ben Davis leaves did not materially vary from the first to the second periods, but they showed considerable rise in the third period.

The rusted Ben Davis leaves used in the experiments had an average of 7.7 infections per sq. cm.; the York leaves had an average of 5.7 per sq. cm.

Part of the improvement in unit transpiration observed in August is no doubt due to the fact that the most seriously infected leaves (comparable to those used in the foregoing periods) had fallen off, and less seriously infected leaves were used as test objects.

Attention may also be directed to the problem of diminished unit transpiration of these diseased leaves and its causes. The

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fungus may work in one or more ways to diminish transpiration, either by its intoxicating action upon the host cells or by causing hypertrophy which alters the normal activities of the leaves. Each of these problems is at present the subject of further investigations. Without going into a study of the cytomorphology of the diseased leaves at this time, it may be said that the portions of the apple leaves bearing cluster cups are three to four times the normal thickness. Their hypertrophy is, as REYNOLDS[6] has reported, chiefly the result of changes in the spongy tissue (parenchyma), by which the loose tissue with large intercellular spaces is replaced by large columnar cells with no intercellular spaces. Stomata are scarce or lacking and the substomatal cavities are altogether lacking. This closure of the intercellular spaces of the leaf diminishes the opportunity for water elimination from the interior of the leaf and consequently affects the transpiration. This may account for the difference between our results and those of BLODGETT previously cited. In the case of the leaves attacked by *G. interstitialis*, the destruction of the lower epidermis facilitates loss of water; while in the apple leaves attacked by *Gymnosporangium Juniperi-virginianae*, the hypertrophy obliterates the stomata and retards the elimination of water.

The retardation of transpiration in the apple leaves studied is believed to have some significance for the study of the real problems concerned with this disease. It has for a long time been known that transpiration and growth are intimately associated. Growth does not usually occur without transpiration. LIVINGSTON[7] and others have shown that in certain instances, at least, transpiration is a reliable index of growth.

Further studies are being made upon the economy of diseased trees, but it is considered that the decreased transpiration of leaves affected with the cedar rust is one factor which may account for the bad physiological condition of such trees.

VIRGINIA AGRICULTURAL EXPERIMENT STATION
BLACKSBURG, VA.

[6] REYNOLDS, E. S., Studies of parasitized leaf tissue. BOT. GAZ. 53:365. 1912.

[7] LIVINGSTON, B. E., Relation of transpiration to growth in wheat. BOT. GAZ. 40:178. 1905.

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UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS XXXVI[1]

JOHN DONNELL SMITH

Rheedia paniculata Donn. Sm.—Folia coriacea orbiculari-obovata basi attenuata remote crasseque penninervia, nervis transversalibus venisque immersis. Flores paniculati, pedicellis singulis. Ovarium 5-loculare.

Ramuli terminales digitum crassi foveolis mutue applicatis apiculati cicatricibus foliorum obovatis 8 mm. longis notati, internodiis 2–3 cm. longis. Folia solum superiora visa 19–24 cm. longa 15–19 cm. lata apice rotundata in siccis concoloria pallide lutescentia nervis fuscentia, nervo mediano supra complanato subtus triangulari, nervis lateralibus ab eo sub angulo fere recto abeuntibus utrinque 11–12 inter se 15–22 mm. distantibus subrectis pone marginem evanescentibus, petiolis 3–4 cm. longis canaliculatis basi incrassata amplexicaulibus in axilla foveola valde prominente ovali 9 mm. longa appendiculatis. Paniculae ad cicatricem foliorum 2–4nae-pedunculo 1.5–3.5 cm. longo computato 4–6 cm. longae 1–3–plo trichotomae, axibus quadrangularibus, ramis 4 decussatis, pedicellis 6 mm. longis medio bibracteolatis, bracteolis semi-orbicularibus 1 mm. longis. Sepala obtuse ovata 2 mm. longa. Petala concava oblongo-elliptica 4.5–5.5 mm. longa uti sepala sub anthesi reflexa. Stamina sub disco inserta usque ad 51, filamentis 3 mm. longis. Ovarium ovoideum 5-sulcatum, stylo brevissimo, stigmate 5–lobo. Bacca ignota.

Inter rivulos *Unión* et *Del Convento* dictos in valle Diquís, Comarca de Puntarenas, Costa Rica, alt. 800, Febr. 1898, *H. Pittier* n. 11957.

Caryocar costaricense Donn. Sm.—Folia oblongo-elliptica obtuse acuminata basi acuta vel obtusa subintegra subtus nervis barbata. Stipellae majores ovatae tenuiter acuminatae concavae basi saccatae, minores orbiculares cucullatae. Racemus pubescens, pedicellis suberectis, prophyllis obsoletis.

Arbor vasta ex schedula Pittieriana, ramulis teretibus sicut petioli petioluli pedunculi pedicelli strigilloso-pubescentibus, internodiis 4.5–7 cm. longis. Foliola terna 10–13.5 cm. longa 4.5–7 cm. lata pergamentacea supra glabra venulis pellucida obscure repanda, nervis lateralibus utrinque 10–12, petiolo communi 5–8.5 cm. longo, petiolulis purpurascentibus 3–4 mm. longis. Stipellae 4 persistentes, 2 majoribus 5 mm. longis ceterao dimidio minores

[1] Continued from BOT. GAZ. 54:235. 1912.

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involucrantibus. Pedunculus 9.5 cm. longus 5 mm. crassus, racemo corymbiformi floribus exemptis 5 cm. longo, rhachi 3 cm. longa, pedicellis circiter 15 robustis 3–4 cm. longis, floribus glabris allium olentibus (cl. repertor in scheda). Calyx 4.5 mm. altus 5.5 mm. latus, basi incrassata explanata, lobis semiorbicularibus 3 mm. longis. Petala 5 obovato-oblonga 18–21 mm. longa lutea margine scariosa integra. Stamina 1.5–2 cm. longa, filamentis totis ob glandulas quasi monilliformibus, antheris ellipticis aegre 1 mm. longis. Ovarium 4-loculare, stylis 11 mm. longis. Drupa ignota.—*C. glabro* Pers. proximum.—Ab incolis *Ajo* (Latine *Allium*) vocatur.

Río del Volcán, in valle Diquís, Comarca de Puntarenas, Costa Rica, alt. 250 m., Febr. 1898, *H. Pittier* n. 12115.

Maytenus enantiophyllus Donn. Sm.—Folia opposita ovato-lanceolata crenato-serrulata. Cymae longe pedunculatae semel bisve trichotomae, axibus capillaribus, floribus tetrameris. Ovarium 4-loculare, ovulis geminis supérpositis, stylo brevissimo, stigmate subintegro. Capsula 2–3-locularis loculicida, seminibus singulis.

Arbor 7-metralis omnibus in partibus glabra, ramulis subtetragonis. Folia pergamentacea opaca subtus glandulis sanguineis passim punctata 8–11 cm. longa 2.5–3.5 cm. lata elongato-acuminata apice ipso obtusa basi acutiuscula, crenis glandula apiculatis, petiolo 4–7 mm. longo. Pedunculi gracillimi 2–3.5 cm. longi, cymis plerumque semel furcatis, axibus 6–12 mm. longis, bracteis lineari-lanceolatis 2 mm. longis uti bracteolae minutae sanguineis. Sepala semiorbicularia 1 mm. longa. Petala orbiculari-obovata 4 mm. longa. Stamina ad marginem disci inserta, filamentis e basi glandulari-incrassata subulatis 1 mm. longis recurvis, antheris globosis 0.5 mm.-diametralibus. Discus planus subquadratus 2.5 mm.-diametralis. Ovarium ovoideum 1.5 mm. longum nonnunquam rudimentarium, stylo 0.5 mm. longo, stigmate obscure 4-lobulato. Capsula carnosa virescens subglobosa 1 cm.-diametralis, valvis ultra medium loculicidis, seminibus totis arillo inclusis ellipsoideis 8 mm. longis, testa membranacea coccinea, albumine carnoso.—Species *Mygindam* revocans foliis oppositis anormalis.

Chiul, Depart. Quiché, Guatemala, alt. 2500 m., Apr. 1892, *Heyde et Lux* n. 3087 ex Pl. Guat. etc. quas ed. Donn. Sm.

Meliosma (§ SIMPLICES Warburg) **Tonduzii** Donn. Sm.—Folia oblanceolata 3–3.5-plo longiora quam latiora cuspidato-acuminata in petiolum attenuata integra vel denticulata. Flores singuli pedicellati. Petala exteriora parum inaequalia leviter imbricata calyptratim decidua. Discus obsoletus. Drupa pyriformis obsolete marginata prope basin latere altero tumida.

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Arbor symmetrica ex repertore, ramis ramulisque teretiusculis glabris, gemmis ferrugineo-pilosiusculis. Folia coriacea nitida, juniora 13–18 cm. longa 4–5.5 cm. lata integra, provectiora usque ad 32 cm. longa 9 cm. lata superne minute remoteque denticulata, costa cum nervis lateralibus utrinque 15–17 supra impressa subtus crassiuscule prominente, petiolis glabris 2–3.5 cm. longis basi incrassatis. Paniculae ferrugineo-appressoque-pubescentes 13 cm. longae, ramis primariis 2 inferioribus divaricatis 4.5–7 cm. longis, ceteris sicut secundarii brevissimis, bracteis linearibus 2 mm. longis, pedicellis 1 mm. longis, bracteolis semiorbicularibus imbricatis pubescentibus. Sepala suborbicularia 1 mm. longa herbacea ciliolata basi pubescentia. Petala coriacea orbicularia 3 mm.-diametralia concava glabra, interiora linearia 2 mm. longa glabra staminodiis semiadnata. Ovarium ovoideum 1 mm. longum biloculare, loculis biovulatis, stylo ovarium bis superante suboblique inserto sursum decrescente, stigmate punctiformi. Drupa pedicello 3–6 mm. longo oblique insidens nitida in sicco nigra 24 mm. longa superne 18 mm. lata prope basin 9 mm. lata ad 7 mm. supra basin foveolata et ibidem saepe styli reliquum ferente, endocarpio osseo basi transversim intrusa subbidentata seminifero.—*M. glabratae* Urb. proxima.

In silvis ad Vueltas, Tucurrique, Costa Rica, alt. 650 m., Maj. 1899, *Adolfo Tonduz* n. 13368.—In silvis prope ostium fluminis *Zhorquín* dicti, Talamanca, Costa Rica, Mart. 1894, *Adolfo Tonduz* n. 8584.

Phyllocarpus septentrionalis Donn. Sm.—Foliola 4–6-juga majuscula elliptica utrinque acuta vel obtusiuscula coriacea nitida. Sepala ampla ciliolata, inferioribus ellipticis, summo orbiculari. Vagina staminalis valde obliqua filamentis brevior, antheris parum aequalibus.

Arbor excelsa, ramulis petiolis racemis pubescentibus. Foliola plerumque 5-juga praeter costam et marginem subtus pubescentes glabra per paria deorsum decrescentia, supremis usque ad 8 cm. longis 3.5 cm. latis, infimis circiter 3 cm. longis 2 cm. latis, petiolo communi 1–3.5 cm. longo, stipulis linearibus 7 mm. longis deciduis, rhachi 8–12 cm. longa, petiolulis 1 mm. longis incrassatis. Racemi ad nodos defoliatos 1–4-ni subsessiles, rhachi 10–13 mm. longa, pedicellis 4–7-nis 11–15 mm. longis prope basin articulatis et ibidem bracteolis 2 connatis lanceolatis 2 mm. longis instructis, floribus praeter calycem glabris. Sepala cartilaginea 9–11 mm. longa. Petala tenuiter membranacea, lateralibus summo intimo bis fere majoribus, inferioribus minimis vel deficientibus. Vagina staminalis postice 12 mm. longa antice 9 mm. longa, filamentis 14–17 mm. longis, decimo summo libero 18 mm. longo, antheris 2–2.5 mm. longis. Ovarium lineari-oblongum 5 mm. longum circiter 3-ovulatum, stylo 13 mm. longo, stigmate globoso. Legumen indehiscens 1–2-spermum, dispermum dum adsit usque ad 17 cm. longum 4.5 cm. latum, monospermum 12.5 cm. longum. 4 cm. latum, suturae ala 10–12 mm. lata. Semen ovale 2.5 cm. longum 1.5 cm.

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latum, radicula recta 2.5 mm. longa.—Haec ab specie hactenus unica hemisphaerii meridionalis Americani incola differt inter alia foliolis paucioribus et uti flores majoribus.

Prope Gualán, Depart. Zacapa, Guatemala, alt. 100 m., Febr. 1912, *Wilmatte P. Cockerell;* exemplum tantum floriferum in herbario Musei Nationalis sub numero proprio 1861342 servatur. De hac specie ita in literis scribit cl. repertor, domina oculatissima res novas acute cernens: Arbor usque ad 18–25-metralis ad ripas Río Montagua et secus viam ferream haud rara floribus praecocibus coccineis odoratis speciosissima formicis apibus volucribus frequentissima ab incolis *Guacomaya* vocata.—Exempla foliifera et fructifera eodem loco Maj. 1912 legit *E. Morris*.

Calyptrella cycliophylla Donn. Sm.—Folia suborbicularia deltoideo-cuspidata basi obtusa quinquenervia coriacea subtus glandulis punctulata. Flores breviter pedicellati ebracteolati hexameri. Calyx furfuraceus. Petala lanceolata attenuato-producta breviter unguiculata. Capsula nitida subovoidea 4–5-valvis.

Ramuli fistulosi subtetragoni cum petiolis et panicula ferruginei furfuracei vel glabrescentes. Folia glabra 19–22 cm. longa 15–17 cm. lata, cuspide 5 mm. longa obtusa, nervis transversis 6–12 mm. inter se distantibus, petiolo teretiusculo 6–8 cm. longo. Panicula deltoidea pedunculo 8 cm. longo praetermisso 21 cm. longa, axibus sicut pedunculus tetragonis sulcatis, ramis inferioribus quaternariis, pedicellis 3–7-nis 1–2 mm. longis cum calyce dense griseo-furfuraceis, floribus inapertis lanceolato-ovoideis 5.5 mm. longis, calyptra glabra apice nutante. Calyx subhemisphaericus 2 mm. altus 3 mm. latus 12-costatus. Petala 6 inaequalia 5 mm. longa satis asymmetrica late unguiculata obscure 6-nervia. Stamina 12, antheris 1.5–2 mm. longis filamenta subaequantibus. Ovarium calycem haud superans nitidum sulcatum, stylo 3.5 mm. longo recto. Capsula nigra calyce bis longior 5 mm. longa 3 mm. crassa 4–5-angularis et-sulcata, valvis plerumque 4, seminibus filiformibus 2 mm. longis straminiis.

Secus rivulum prope Buenos Aires, Comarca de Puntarenas, Costa Rica, alt. 280 m., Jan. 1892, *Ad. Tonduz* n. 4964.—Ad ripas fluminis *La Unión* dicti, Comarca de Puntarenas, Costa Rica, Jan. 1897, *H. Pittier* n. 10584.

Gilibertia gonatopoda Donn. Sm.—Folia maxima elliptica obtuse cuspidata basi acuta vel obtusiuscula. Racemi terminales vel laterales, pedunculis crassis sulcatis paulo infra medium pluribracteolatis articulatis geniculatis ceterum nudis. Calyx turbinatus petalis longior. Drupa globosa.

Arbor mediocris, ramulis subteretibus sulcatis. Folia pergamentacea 11–30 cm. longa 5–18 cm. lata integra, nervis lateralibus utrinsecus 9–10 subrectis

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in utraque pagina conspicuis, petiolis canaliculatis sulcatis 2–12 cm. longis, stipulis deciduis. Racemi floriferi rhachis 4–5 cm. longa, pedunculi 8–16 circiter 2.5–3.5 cm. longi epidermate transversim rimulosi ad articulationem nodosam bracteolis 4–6 rotundatis 1 mm. altis circumdati, receptaculum parce minuteque bracteolatum, pedicelli 25–40 circiter 8–11 mm. longi, flores pentameri 4.5–5 mm. longi. Calyx 2.5–3 mm. longus 2 mm. latus margine subinteger. Petala subcarnosa ovata 2 mm. longa acuta 1-nervia staminibus subaequilonga. Discus hemisphaericus 1.5 mm.-diametralis. Styli in conum 0.5 mm. altum toti connati. Drupae optime globosae 4 mm.-diametrales columna stylari 1 mm. longa disci dimidium aequante coronatae.

Ad ripas fluminis *Turrialba* dicti, Prov. Cartago, Costa Rica, alt. 500 m., Mart. 1894, *John Donnell Smith* n. 4829 ex Pl. Guat. etc. quas ed. Donn. Sm. —In silvis prope flumen *Zhorquin* dictum, Talamanca, Costa Rica, alt. 200 m., Mart. 1894, *A. Tonduz* n. 8512.—In silvis ad Shirores, Talamanca, Costa Rica, alt. 100 m., Febr. 1895, *A. Tonduz* n. 9323.—In silvis apud Tsaki, Talamanca, Costa Rica, alt. 200 m., Apr. 1895, *A. Tonduz* n. 9587.—Ad marginem fluminis *Del Convento* dicti, in valle Diquís, Comarca de Puntarenas, Costa Rica, Mart. 1898, *H. Pittier* n. 12110. Secus fluvium *Las Vueltas* dictum, Tucurrique, Costa Rica, alt. 635 m., Jan. 1899, *A. Tonduz* n. 12962.

Gilibertia stenocarpa Donn. Sm.—Folia alia indivisa oblongo-ovata vel-elliptica, alia ad medium fere trilobata, lobo terminali rotundato cuspidato, lateralibus acuminatis. Umbellae racemosae, pedicellis flores vix aequantibus. Drupa elliptica triente longior quam latior.

Arbor 10–15-metralis. Folia membranacea subtus glandulis rubellis punctulata margine integra circumscriptione quam maxime variabilia, nempe: indivisa 12–16 cm. longa 6–11 cm. lata acuminata basi cuneata utrinque 6–7-penninervia, folia lobata cum praecedentibus intermixta ambitu rhomboidea suborbicularia vel transversim ovalia 11–17 cm. longa 8–20 cm. lata triplinervia, lobo terminali maximo 6–9.5 cm. longo 4–7 cm. lato dimidio superiore plerumque semiorbiculari, lateralibus subtriangularibus vel acuminato-ovatis 2–6.5 cm. longis atque latis, altero insolenter obsoleto. Petioli 5–22 cm. longi. Stipulae minimae rubiginoso-pubescentes. Inflorescentia terminalis. Racemi floriferi rhachis juvenilis rubiginoso-pubescens, adulta 4 cm. longa, pedunculi 16–21 circiter 2 cm. longi parce dissite minuteque bracteolati, receptaculi bracteolae rubiginoso-pubescentes, pedicelli 2.5–3 mm. longi, floreres usque ad 45 pentameri 3.5 mm. longi. Calyx obpyramidalis 1.5 mm. altus atque latus minute denticulatus. Petala ovata 1.5 mm. longa scariosa staminibus paulo superata. Styli in conum 1 mm. fere altum disci dimidium aequantem toti connati. Drupae 6 mm. longae 4 mm. crassae columna stylari 2 mm. fere longa coronatae.

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In praeruptis *Barranca de Eminencia* dictis, Depart. Amatitlán, Guatemala, alt. 1200 m., Febr. 1892, *John Donnell Smith* n. 2666 ex Pl. Guat. etc. quas ed. Donn. Sm.—Santa Rosa, Depart. Santa Rosa, Guatemala, alt. 1300 m., Maj. 1892, *Heyde et Lux* n. 3348 ex Pl. Guat. etc. quas ed. Donn. Sm.—El Salvador, loco accuratius haud addicto, *Carlos Rénson* n. 66 (Exemplum in herb. Musei Nationalis numero proprio 576040 signatum vidi.)

Gilibertiae species in America Centrali obviae ad inflorescentiam ceteris characteribus neglectis dignosci possunt, nempe:

I. Umbella solitaria. *G. querceti* Donn. Sm. (*Dendropanax querceti* Donn. Sm.)
II. Umbellae racemosae.
  A. Pedunculi medio articulati. *G. gonatopoda* Donn. Sm.
  B. Pedunculi inarticulati.
    1. Pedicelli flores vix aequantes. *G. stenocarpa* Donn. Sm.
    2. Pedicelli flores superantes.
      a. Umbellae 25–40-florae. *G. arborea* E. March.
      b. Umbellae 10–20-florae. *G. Rothschuhii* Harms.

Basanacantha (?) **grandifolia** Donn. Sm.—Inermis. Folia coriacea permaxima lanceolato-vel elliptico-oblonga utrinque acuta. Stipulae numerosissime imbricatae scariosae minimae in bracteas transientes. Flores masculini pluri-aggregati subsessiles, calyce bracteis imbricatis fere velato breviter dentato.

Tota stipulis praetermissis glabra. Ramuli teretes. Folia tantum suprema obvia bina 28–32 cm. longa 9–14.5 cm. lata saepius falcata utrinque nitida subtus elevato-punctulata, nervis lateralibus utrinsecus 10–12 arcuatim anastomosantibus, petiolo canaliculato 2.5–3.5 cm. longo. Stipulae apicem interpetiolarem ramulorum obtegentes leviter cohaerentes ferrugineae late ovatae 4 mm. longae mucrone nigro cuspidatae extus punctulatae intus elongato-glandulosae et cano-villosae. Flores solum masculini visi subcapitulati, pedicellis crassis 1.5 mm. longis. Calyx campanulatus 3 mm. longus, dentibus subulatis 1 mm. longis margine scarioso connexis. Corolla hypocraterimorpha, tubo 5-sulcato 12 mm. longo, lobis acuminato-ovatis 7 mm. longis. Antherae inclusae subsessiles lineares 5 mm. longae apice obtusae basi retusae paulo infra medium affixae. Discus elevato-pulvinaris 1.5 mm. altus 2 mm. latus centro intrusus. Ovarii rudimentum nullum, stylo 11 mm. longo triente bifido. Bacca ignota.—Species habitu stipulisque insignis et fortasse melius genus proprium censenda.

In silvis prope Santo Domingo, Golfo Dulce, Comarca de Puntarenas, Costa Rica, Febr. 1896, *Adolfo Tonduz* n. 9878.—Ad ripas fluminis *Corozal* dicti, prope Santo Domingo, Golfo Dulce, Costa Rica, Apr. 1896, *Adolfo Tonduz* n. 9982.

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Perymenium ruacophilum Donn. Sm.—Folia lanceolato-ovata basi acuta trinervia serrulata supra scabridiuscula subtus glabrescentia. Corymbi remote patenterque ramosi, pedicellis trinis. Involucri bracteae 3–seriatae oblongae obtusae superne fimbrillatae. Receptaculum conicum.

Rami cum ramulis remotissimis brachiatis teretiusculi sulcati glabri purpurascentes, gemmis axillaribus cano-pilosis. Folia membranacea 6.5–9 cm. longa 2–5 cm. lata tenuiter acuminata e basi ipsa trinervia calloso-serrulata, petiolis 1.5–2.5 cm. longis pubescentibus linea pubescente connexis. Corymbi glabrescentes inferne foliis reductis ceterum bracteolis linearibus 2–5 mm. longis pubescentibus instructi, eorum bene evolutorum rhachi 2.5 cm. longa, ramis inferioribus 2.5 cm. longis, pedicellis circiter 1.5 cm. longis dissite et saepe sub capitulo bracteolatis. Capitula oblongo-obovata 10–11 mm. longa, involucri bracteis apice purpurascentibus margine membranaceo lacerato minute fimbrillatis, intimis 6 mm. longis, extimis 3 mm. longis, receptaculo 2 mm. alto atque lato, paleis flores parum amplectantibus 6–7 mm. longis acuminatis minute ciliolatis. Ligulae 6–7 circiter 9–10 mm. longae 2–3-denticulatae. Flores disci numerosi 8 mm. longi. Achenia compresso-triquetra 2 mm. longa glabra deorsum angustiora basi callosa, maturis calvis, pappi aristis numerosis distinctis ciliolatis caducissimis.

In monte *Volcán Santa Maria* dicto, Depart. Quezaltenango, Guatemala, alt. 2500–3500 m., Jan. 1896, *E. W. Nelson* n. 3727.

Arctostaphylos (§ EUARCTOSTAPHYLOS Drude.) **cratericola** Donn. Sm.—(*A. pungens* H.B. et K., var. *cratericola* Donn. Sm. in BOT. GAZ. **15**:13. 1891.)—Folia glabra obovata vel obovato-elliptica calloso-apiculata subtus punctulata. Racemi puberuli, pedicellis flore 2–3-plo brevioribus. Filamenta nuda corolla 3-plo breviora antheris bis longiora, aristis antherae aequilongis.

Fruticulus coespitosus, caulibus prostratis 3–4 dm. longis ramosis dense foliatis fuscis cortice exfoliantibus, ramulis apice trigonis puberulis ceterum glabris. Folia 14–20 mm. longa 9–10 mm. lata leviter induplicativa minute reticulata rosaceo-apiculata passim rosaceo-maculata, juniora margine puberula, petiolis 2–3 mm. longis puberulis. Racemi subsessiles nutantes subcapituliformes 6–8-flori erubescentes, pedicellis 2–3 mm. longis, bractea exteriore lineari-lanceolata 5 mm. longa. Calycis segmenta suborbiculata 2 mm. longa ciliolata rosacea. Corolla urceolata, tubo 6 mm. longo albido, dentibus semiorbiculatis 1 mm. longis reflexis rosaceis. Filamenta 2 mm. longa infra medium suborbiculari-dilatata. Discus 10-sulcatus. Ovarium 5-loculare stylo addito corollae tubum fere aequans. Drupa ignota.

Ad rupes in cratere, Volcán de Agua, Depart. Zacatepéquez, Guatemala,

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alt. 3600 m., Apr. 1890, *John Donnell Smith* n. 2159 ex Pl. Guat. etc. quas ed Donn. Sm.—Volcán de Agua, Depart. Zacatepéquez, Guatemala, alt. 2700–3100 m., Febr. 1905, *W. A. Kellerman* nn. 4754, 4950.

Cordia gualanensis Donn. Sm.—Folia inter minima ex ovali ovata vel oblongo-ovata cuspidata integra supra scabrida subtus strigillosa. Cymae terminales folia subaequantes. Calyx esulcatus, dentibus 5 subulatis brevibus. Corolla infundibularis, tubo quam calyx bis quam lobi dimidio longiore. Stamina 4–8.

Frutex ut videtur, ramis teretibus glabris. Folia 18–31 mm. longa 12–18 mm. lata, nervis lateralibus utrinque 6–7 uti venae transversales subparallelae inter se 1–2 mm. distantes et costa fuscentibus, petiolis 1–4 mm. longis. Cymae nondum satis evolutae solum visae terminales et ad apicem ramulorum brevissimorum foliis juvenilibus instructorum pseudo-axillares fusco-velutinae 9–12-florae, pedunculo 2–3-mm. longo, rhachi 10–13 mm. longa. Calyx subsessilis campanulatus extus fulvo-sericeus intus puberulus 5-costatus minute reticulatus, tubo 5 mm. longo, dentibus 1 mm. longis. Corollae puberulae tubus, 11–12 mm. longus, lobi 4–8 obovati 7 mm. longi. Stamina usque ad medium fere corollae tubum et subaequaliter affixa saepe inaequilonga, antheris inclusis vel breviter exsertis cordiformibus 1.5 mm. longis retroversis. Ovarium pyramidale 2 mm. longum glabrum, stylo 7 mm. longo triente bifido, ramis dimidio bifidis, stigmatibus clavatis. Drupa deficiens.

Gualán, Depart. Zacapa, Guatemala, alt. 122 m., Mart. 1905, *W. A. Kellerman* n. 5105. (Exemplum in herb. Musei Nationalis numero proprio 576295 signatum exstat.)

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VEGETATIVE REPRODUCTION IN AN EPHEDRA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 172

W. J. G. LAND

(WITH FIVE FIGURES)

When the branches of many plants are covered with soil or even make contact with it, they may put out roots and produce new plants. This method of reproduction is common among angiosperms and to a less degree among gymnosperms, where heretofore it has been reported only for Coniferales. Many species, distributed among *Abies*, *Picea*, *Pinus*, *Larix*, *Pseudotsuga*, *Thuja*, *Chamaecyparis*, and *Cryptomeria*, produce new plants by the rooting of horizontal branches which then either erect the tip of the rooting branch or send out erect lateral shoots. The unfortunate term "layering" has been applied to this method of vegetative reproduction.

The latest account for a gymnosperm is that of COOPER[1], who describes "layering" in *Abies balsamea* and cites the scanty literature of the subject.

Until now no special method of vegetative reproduction has been reported for Gnetales, perhaps because the relative inaccessibility of the group has prevented careful field studies.

In September 1911 occasional clumps of an *Ephedra* were found on the very steep rocky sides of the cañon of Rifle Creek, near the southern boundary of the White River forest reserve in western Colorado. This *Ephedra* is probably conspecific with *E. nevadensis*, although differing from the latter in some minor characters.

Rifle Creek, where it falls over the edge of the White River plateau, for some miles has carved out of very hard limestone a box cañon with walls in some places rising perpendicularly to a height of more than 150 meters (fig. 1), or even leaning outward over the cañon floor. Emerging from the box cañon the stream flows for

[1] COOPER, WILLIAM S., Reproduction by layering among conifers. BOT. GAZ. 52:369–379. *fig. 1.* 1911.

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a short distance through soft limestone with regular slopes steeply V-shaped, then through sandstone conglomerate, which being very friable weathers rapidly. The faces of the sandstone slopes show a series of low cliffs (fig. 2) alternating with nearly bare talus. The walls of the cañon are exceedingly unstable.

Ephedra is sparsely distributed along the cañon walls for nearly four miles, occurring only on the most exposed and most unstable slopes in clumps of from four or five plants to sometimes twenty

FIG. 1.—Limestone cliff at entrance to the box cañon of Rifle Creek, near the upper limit of *Ephedra*, which is found in small quantities at the top and in the talus slope at the base.

or infrequently more. Isolated plants are rare and an examination of one of these showed that it had been torn from a clump on a cliff above by a small landslide. The vertical range is as sharply limited as is the horizontal, no plants being found at an altitude below 2000 nor above 2200 meters. The clusters are most abundant on the sandstone slopes, the greatest display and most vigorous plants being near the lower limiting altitude (fig. 2); thence running up the ridges between the small side cañons and becoming

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fewer and fewer until they completely disappear at 2200 meters. Rarely plants are found growing in the scanty bowlder-strewn soil on ledges along the face of the limestone walls of the box cañon. In one instance a small clump was seen on the extreme edge of the great cliff (fig. 1) which towers above the cañon floor. In the coarse limestone talus at its base were a few plants, much battered by falling stones. This cliff, rising almost to the vertical range of *Ephedra* is capped by a steep ridge of the coarse friable sand-

FIG. 2.—*Ephedra* on sandstone talus near lower limiting altitude; dead *Pinus edulis* in foreground; a typical situation.

stone of the lower cañon. Here also were a few small clumps of depauperate plants. *Ephedra* was not found on the relatively moist, well-wooded north slopes nor in the cañons of adjacent watercourses, but the rough nature of the country made extended search somewhat difficult.

Some plants reach a height of 2.5 meters, and below the first branching, which is usually at the surface of the soil, may attain a diameter of 10 cm. The largest trunk found (fig. 3) had a diameter of 5 cm. just above the first fork. The greatest number of seasonal

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rings found was 40, showing that the plant is comparatively short-lived.

Associated with *Ephedra* are occasional plants of *Artemisia tridentata*, the older ones much battered by snowslides and rolling stones, and quantities of *Cercocarpus parvifolius*, the mountain mahogany. Rarely indeed in the sandstone talus a plant of *Equisetum* is found. On more stable slopes *Pinus edulis* and species of *Juniperus* are fairly abundant. The general instability of the

FIG. 3.—An old *Ephedra* on a comparatively stable slope; the oldest plant found in the region, having 40 growth rings.

region is well shown in fig. 2, where a pine has perished because of the rapid wearing away of the sandstone cliff.

A careful and persistent search throughout the range of *Ephedra* was made for seedlings, but since none could be found, it seemed evident that such a short-lived plant, in order to maintain itself under the severe conditions imposed by its habitat, must have some method of vegetative reproduction. The almost universal occurrence of clumps led to a careful examination of the underground condition. In nearly every instance it was found that the

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individuals of a group are either actually connected by means of underground stems or that traces of a former connection could be made out. Sections show that these underground connections are stems and not roots.

Large boulders and masses of friable rocks are continually being detached from the cañon walls, and these, together with deep accumulations of snow, are sufficient to overthrow even the largest plants of *Ephedra*, as is shown in fig. 4. At the right, in this figure,

FIG. 4.—A clump of *Ephedra* showing large plants being overthrown by boulders

two boulders are bending down one of the largest plants of the clump. The branches of this plant will finally be forced into contact with the soil, most likely be covered with talus, take root, and give rise to a new cluster of plants. An almost completely decayed trunk was found under the boulder shown at the extreme left of the figure. This trunk had given rise to a small clump not shown. Young plants are so slender that they are easily overthrown and buried by small landslides. On a loose and rapidly moving slope composed of small stones and coarse sand, underground connections were traced for 5 meters. The oldest plant showing five

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seasonal rings was above and the younger ones farther down the slope, stretched out in an almost straight line by the flowing talus. After a stem has been buried it is sometimes difficult to detect the growth of succeeding seasons.

Underground stems rising from stems which have been buried for some years were found creeping among the loose stones and coarse sand of the sandstone slopes. These shoots are, in effect, rhizomes which later produce aerial shoots either by branching or by erecting

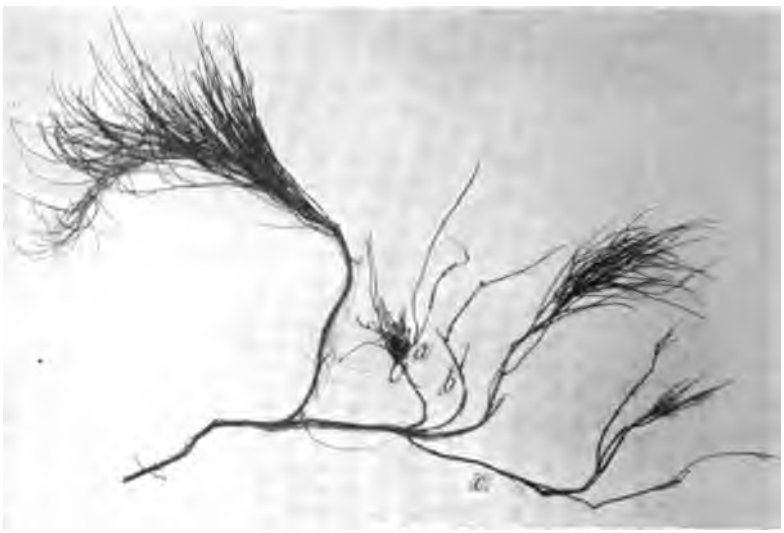

FIG. 5.—Underground connections of a small clump of *Ephedra* found in the talus shown at the extreme right of fig. 2; *a*, young rhizome; *b*, older rhizome which has sent up an aerial shoot; *c*, rhizomes which have erected their stem tips.

the main stem tip, or by both methods. The rhizome habit is shown in fig. 5. The branched underground shoot *a*, springing from the buried stem which has also given rise to the damaged cluster of aerial branches, has grown in one season (1911). At *b* is an older stem which has produced an aerial branch. At *c* is a stem which has branched, and the branches, after a time, have become aerial by erecting their tips. The rhizomatous branches were not found where the soil is compact, being only in loose sand and small stones. It seems worthy of note that the soil above 2200 meters, the upper

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limiting altitude of *Ephedra*, is compact. Since the tendency of soil movement is to force the plant constantly toward lower altitudes, if it were not for underground lateral branching, *Ephedra* would first be driven from the higher slopes and ultimately from the region.

If *Ephedra* does produce seeds in this region they are promptly destroyed by small animals. Not many seedlings of pine and spruce are found, although great quantities of seeds mature. Spruce seeds are eaten by squirrels as soon as they ripen and long before they fall. Great numbers of piñon jays visit the region in autumn and feed on the nuts of *Pinus edulis*. However, piñons and spruces are so abundant that enough seeds to keep up the forest are overlooked. It is regretted that observations cannot soon be made to determine if *Ephedra* really does set seed in this region.

Most of the branches of this *Ephedra* fall at the close of summer, a regular absciss layer being developed at each node. In September the ground under the plants is green with the fallen branches.

Ephedra nevadensis was found in western Colorado only on the most bleak and unstable slopes and does not seem to be widely distributed. No seedlings were found. The plant propagates itself vegetatively by shoots, which, after having been overthrown and buried by talus, take root, erect their tips, and send out erect lateral branches; and also by means of underground rhizomes which are given off from older buried shoots. These rhizomes either send up branches or erect their tips or they may do both. They may also send out other rhizomes. Assuming the absence of seeds, *Ephedra* owes its preservation in this region to the rhizome-forming habit. If it were not for this habit and if other factors which are not apparent at present did not intervene, soil movement would ultimately force the plant below the lower limiting altitude and cause it to disappear entirely from the region.

University of Chicago

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PROTOPLASMIC CONTRACTIONS RESEMBLING PLASMOLYSIS WHICH ARE CAUSED BY PURE DISTILLED WATER

W. J. V. Osterhout

(WITH SIX FIGURES)

True plasmolysis is produced only by solutions which are hypertonic, but appearances almost or quite indistinguishable from it may be brought about by hypotonic solutions.[1] Some light is thrown on the nature of this result by a study of certain cases in which it is caused by pure distilled water.[2]

Material for such study is afforded by marine plants. The root tips of the eel-grass (*Zostera marina*) are well adapted to this purpose. The roots were carefully removed from the sand in which they were growing and immediately placed in sea water. Some of the younger roots (which had not yet become brown at the end) were selected. About an inch of the root tip was removed and placed on a hollow-ground slide in such a way that the young root hairs did not come into contact with the glass. The root tip was covered with sea water and examined without a cover glass (by means of an 8 mm. objective and an ocular magnifying ten times). Root tips which were shown by such examination to be normal in appearance were fastened by means of vaseline to cover glasses which were then attached to irrigation chambers of the form shown in fig. 1. Care was taken to prevent the young root hairs from touching the glass or the vaseline.

The arrangement of the apparatus may be understood from figs. 1 and 2. The irrigation chamber consists of an ordinary

[1] Cf. Bot. Gaz. 46:53. 1908.

[2] Water twice distilled from glass is usually regarded as pure, especially when the first and last thirds of the distillate are rejected, but such water may be toxic to plants as long as any part of the apparatus is new. The water used in these experiments was prepared with due regard to these facts. In place of stoppers, plugs of absorbent cotton were used; contamination by spattering was prevented by baffling plates of glass and glass wool. The water so obtained was not toxic to such test objects as sensitive species of *Spirogyra* and the root hairs of *Gypsophila*.

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glass slide with a circular opening (15 mm. in diameter) into which is fitted a glass cylinder (*c*) 12 mm. high upon which is cemented a glass disc (*d*); surrounding this is another cylinder, the width of the space between the two being about 1 mm.; a part of this space is filled with paraffin (*e*). The outer cylinder is pierced on both sides by small glass tubes (*b*, *b*). The outer cylinder projects above the inner so that when the cover glass (*f*) is in place the width of the space between (*d*) and (*f*) is a little less than 1 mm. It is necessary to have this space narrow, since otherwise when introducing a solution of greater specific gravity than the one with which the chamber is filled, the new solution may flow over the bottom of the space without coming into contact with the plants, which are fastened to the under side of the cover glass. The paraffin (*e*) extends downward to the slide; the liquid is in consequence obliged to pass upward through the space between (*d*) and (*f*) before it can flow out at the opposite side, and it must therefore bathe the plants which are attached to the cover glass (*f*).

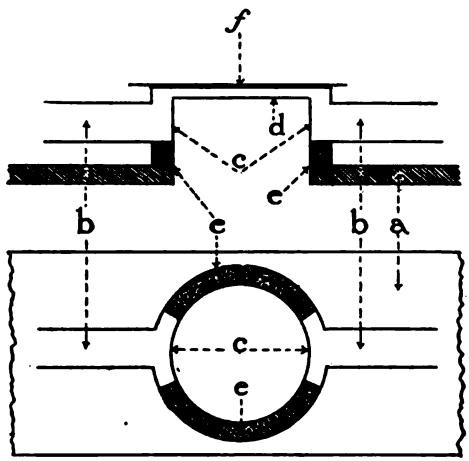

FIG. 1.—Sectional views of irrigation chamber: *a*, slide; *b*, inlet and outlet tubes; *c*, glass cylinder; *d*, glass plate; *f*, cover glass (upper line) and material (lower line).

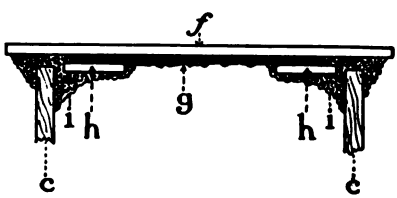

FIG. 2.—Material in irrigation chamber: *c*, glass cylinder; *f*, cover glass; *g*, material; *h*, bits of cover glass; *i*, vaseline. —Sectional view.

The attachment is made in the manner shown in fig. 2. The plant is first fastened to the cover glass (*f*) by vaseline (*i*, indicated by the dotted area) and a drop

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of sea water is placed on it; bits of cover glass (*h*, *h*) are then thickly covered with vaseline, and pressed down upon it to hold it in place. The outer cylinder is smeared with vaseline and sea water is then poured into a funnel which is connected by a rubber tube with the inlet tube (*b*); as soon as all the air has been expelled from this tube and the chamber is so full of sea water that the surface of the liquid is decidedly convex, the cover glass (with the attached root tip) is inverted and pressed down upon the outer cylinder in the manner shown in the figure. Care should be taken during the subsequent irrigation not to admit air to the inlet tube.

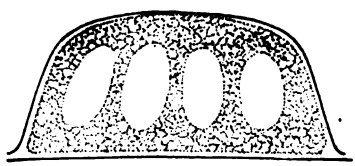

FIG. 3

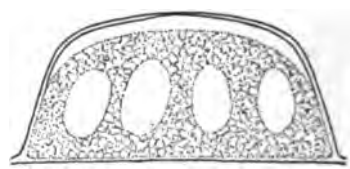

FIG. 4

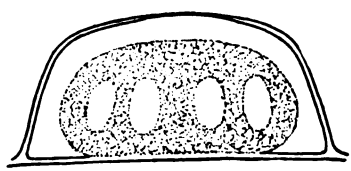

FIG. 5

FIGS. 3–5.—Optical section of young root hair cell of *Zostera marina* (diagrammatic); fig. 4, the cell shown in fig. 3 after treatment with distilled water (diagrammatic); fig. 5, the cell shown in fig. 4 after more prolonged treatment with distilled water (diagrammatic).

After being placed in the chamber, the root tips were irrigated for a time with sea water while camera lucida sketches were made of root hairs in various stages of development. Each of the cells which had been sketched was than kept under observation during the subsequent irrigation with distilled water. Root tips which were irrigated with sea water throughout the experiment served as controls.

The application of distilled water causes a contraction of the protoplasm which often closely resembles the true plasmolysis produced by hypertonic sea water (which has been concentrated by evaporation) or by hypertonic sugar solutions. Figs. 4 and 5 show the appearance of such cells. The mode and the degree

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of contraction vary somewhat, but in general the variations in true plasmolysis are of the same sort as in what may be conveniently called the false plasmolysis. We may use the term "false plasmolysis" to designate not only the contraction produced by distilled water but also that which is caused by hypotonic solutions.

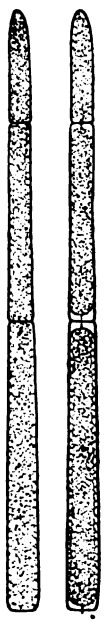

FIG. 6.—Surface view of the end of a hair of *Polysiphonia violacea:* at the left in natural condition; at the right after treatment for two minutes with distilled water (diagrammatic).

The contraction may take place rather slowly, in many cases requiring half an hour or more to reach the stage shown in fig. 4. True plasmolysis may take place much more rapidly. But this distinction does not hold generally, for in many cases contractions which closely simulate true plasmolysis may take place with great rapidity. To give a single example of this, the behavior of the colorless terminal cells and of hairs of *Polysiphonia violacea*[3] may be described. On being irrigated with distilled water these cells contract very rapidly, so that at the end of two minutes they reach the stage shown at the right in fig. 6, in which they are practically indistinguishable from cells plasmolyzed by hypertonic sea water or hypertonic sugar solutions. The older cells reach the same stage more slowly and betray by the alteration of their chromatophores that they are undergoing false plasmolysis. It should be noted that by applying hypertonic solutions of many salts, both true and false plasmolysis may be produced simultaneously. These contractions are (as a rule) irreversible, at least as soon as they have passed a certain stage.

The effects which have been described as due to distilled water were also produced by water taken directly from ponds, rivers, and springs; they are not due, therefore, to toxic substances resulting from the process of distillation; this point is emphasized because attention has previously been drawn to the

[3] Kindly identified by Dr. W. G. FARLOW.

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fact that water distilled in a metal still produces such results in *Spirogyra*, while pure distilled water does not.

The cause of these effects lies in an increase in the permeability of the plasma membrane (and likewise of internal cell membranes), as the result of which some or all of the substances which maintain the osmotic pressure of the cell diffuse out; the protoplasm then shrinks as the result of loss of water from the vacuoles, which in consequence become smaller, as is shown in figs. 3–5. This is often followed by an apparent "coagulation" of the protoplasm, which is sometimes evidenced by the assumption of an irregular outline. Most of the characteristic features of cytolysis as described for animal cells are lacking. In some cases, however (particularly in cells which are not surrounded by a cell wall), they occur.

These effects might naturally be ascribed to the absorption of water by the protoplasm, but they cannot be due to this cause, for observation shows that the cells do not increase in size as they would if water were absorbed. In some cases a few of the cells burst when transferred to distilled water, but the majority do not burst or even swell noticeably. This is probably due in some cases to the fact that swelling is prevented by the cell wall, for some cells which lack the cell wall (for example, spores of *Polysiphonia*) may swell in distilled water. Moreover, it was found that isotonic solutions of cane sugar produce the same effects as distilled water although not as rapidly.

The increased permeability must be due, therefore, to the loss of certain substances upon which the maintenance of the normal permeability depends. The most important of these are undoubtedly the inorganic salts. If the concentration of salts be lowered beyond a certain point, the permeability of the membrane increases very rapidly. This is shown by experiments in which the increase of permeability is directly measured by electrical means. In sea water plus an equal amount of distilled water the cells do not shrink, but with the addition of three volumes of distilled water they may begin to shrink in seven hours or less, and with increasing amount of distilled water shrinkage takes place more and more rapidly. These remarks apply only to balanced solutions such as sea water.

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The effect of unbalanced solutions on permeability has been discussed elsewhere.[4]

The facts described above have an important bearing on certain theories recently advocated by some biologists and colloid chemists. According to these authors, the effects which are usually attributed to osmotic pressure are in reality due to imbibition or to the giving up of water by the protoplasm, without the intervention of a semipermeable membrane. It would not be possible on this theory to account for the shrinkage of the protoplasm of a cell to half its volume when transferred from sea water to distilled water, especially when the process is irreversible. But the explanation given above—the increase of permeability of a semipermeable membrane—not only agrees with the facts described here, but also with those derived from a variety of other material, and by the use of entirely different methods.

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HARVARD UNIVERSITY

[4] Science, N.S. 35:112. 1912; 36:350. 1912.

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REPRODUCTION BY LAYERING IN THE BLACK SPRUCE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 173

GEORGE D. FULLER

(WITH SIX FIGURES)

During the summer of 1912, while making some ecological studies along the Saguenay River, Quebec, attention was directed

FIG. 1.—The black spruce growing on granite with a basal whorl of prostrate branches; Chicoutimi County, Quebec.

to the process of forest development upon granitic areas with very little soil, where the rocky surface was exposed to the full sweep of the wind. The most careful studies were made on a series of

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granite hills with typical *roches moutonnées* contours and with elevations varying from 100 to 200 meters, in Chicoutimi County, bordering an arm of the river known as Ha! Ha! Bay. In these exposed situations there occurred a characteristic pioneer forest association consisting, as far as its tree species were concerned, of black spruce (*Picea mariana* Mill. BSP.), Jack pine (*Pinus Banksiana* Lamb.), the white birch (*Betula alba papyrifera* (March.) Spach.), and the aspen (*Populus tremuloides* Michx.), together with occasional trees

FIG. 2.—The prostrate branches of the black spruce rooting in the mat of mosses and lichens and producing upright shoots; one such shoot has been provided with a white background.

of a few other species. Because of the slow weathering of these areas, the pioneer stages of forestation were much prolonged, but appeared to be promoted by the development of a peculiar growth habit and a resulting vegetative reproduction by layering. This habit was most highly developed and occurred most frequently in the black spruce.

Grown in swamps or thickets the black spruce is characterized by a narrow irregular cone of branches. This cone was found to be

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even more slender in the sparse stand upon the granite surfaces, but in these open situations there were in addition to the short branches on the upper part of the trunk longer ones near the surface of the rock (figs. 1 and 2), forming a compact mat, none of the twigs more than half a meter high. At least one-half of the total foliage of the trees was usually upon these prostrate branches, and it would seem from the apparent vigor of the leaves that an even larger proportion of the work of food synthesis was to

FIG. 3.—A dead stump of black spruce with a circle of living offspring from its layered branches.

be referred to this lower stratum. The rooting of the trees in these rocky habitats was, as a rule, very shallow, and hence the massing of their branches reduced the exposure to winds and the consequent danger of uprooting. The habit was necessarily confined to open stands.

The mat of lichens and mosses which antedated the tree continued to thrive under and among the prostrate branches and the resulting soil soon buried portions of the lower members of the mass. On *Pinus Banksiana* this was apparently without results other than

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FIG. 4.—A rooted branch of black spruce the result of layering; the upright shoot is the one with the white background in fig. 2.

FIG. 5.—A layered branch of black spruce

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somewhat more securely anchoring the trees, but on the spruces it often stimulated the production of roots from the buried branches and caused a circle of young trees to surround the parent (fig. 2).

Such reproduction in conifers was recently discussed by COOPER,[1] who also gave very complete citations of the scanty literature of the subject. The layering habit in *Picea mariana* has been mentioned by LOUDON,[2] for specimens growing under partial cultivation on the British Isles, but its importance in increasing the stand upon

FIG. 6.—A group of young black spruce descended by layering from a single parent tree; the remains of the dead parent are concealed by the young trees; Chicoutimi County, Quebec.

rocky areas seems to have escaped notice. The fact that the rate of growth has been found to be very slow in such localities[3] makes such a method of rapid multiplication and replacement an even greater advantage to the species possessing it. Should trees

[1] COOPER, W. S., Reproduction by layering among conifers. BOT. GAZ. 52:369–379. 1911.

[2] LOUDON, J. C., Arboretum et Fruticetum Britannicum. London. 1844.

[3] COOPER, W. S., The climax forest of Isle Royale, Lake Superior, and its development. II. BOT. GAZ. 55:115–140. 1913.

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of the black spruce growing on granite be cut down, their early replacement is much more definitely assured (fig. 3).

By this layering circular areas with a radius of 2–4 meters soon become covered with vigorous young upright shoots, like the one provided with a white background in fig. 2, which is 2.4 meters from the main trunk. This shoot was removed from the soil and proved to be one of two upon a prostrate branch rooted at several points throughout its length (fig. 4). The orthotropic development of the shoot is well marked, while several other twigs showed it in a less marked degree. The development of such shoots seems to be closely connected with the production of adventitious roots, although not always dependent upon it. Occasionally an abundance of adventitious roots was unaccompanied by any definitely orthotropic shoots (fig. 5). This was frequently noticed in the layering of *Abies balsamea* as it occurs in its shrubby habit in the deeper forests.

The layering was seldom found on *Picea canadensis*, because this species rarely occurs in exposed rocky situations as a member of the pioneer forest association. By far the greatest importance of the habit, in the Saguenay region, is its abundance in the black spruce. Often large clumps of small trees could be referred to the parentage of a few individuals, although with increase in size the connections became increasingly difficult to trace. Frequently clusters of 6–20 closely clustered young trees (fig. 6) marked the spot where a tree of a former generation stood, showing much more rapid replacement than could have been effected by seed.

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BRIEFER ARTICLES

THOMAS HOWELL

(WITH PORTRAIT)

Mr. THOMAS HOWELL, the pioneer botanist of Oregon, died on December 3, 1912, in Portland, at the age of 70 years. He was born near Pisgah, Missouri, October 9, 1842, whence he moved to Oregon in 1850, before railroads had entered the state. Although he received a meager school education, he was a well learned man and an enthusiastic botanist. He did not marry until his 54th year. His wife and a son of seven survive him.

Just before his death he completed the second edition of his *Flora of Northwestern America*, replacing the BENTHAM and HOOKER system with that of ENGLER and PRANTL. This publication embodies the life work of Mr. HOWELL, who spent more than 30 years tramping and traveling over the states of Washington and Oregon. Considering the vast area of these states, and the vicissitudes of pioneer life in that far isolated country, the task of accumulating the data for such a complete flora of the region is realized. Naming the localities worked in these states would require much space; suffice it to say, that the only places he did not visit were portions of central northern Washington and of the central part of Oregon. It is not known to the writer how much material he collected; the Field Museum alone has 2263 specimens. His flora lists and describes about 3290 species. It was the good fortune of Mr. HOWELL to discover and describe the last of the Pacific coast conifers, *Picea Breweriana*, the weeping spruce, a very local tree near the Oregon-California line, which he first found at Waldo, in the Siskiyou Mountains, at an elevation of 6000 feet.

Mr. HOWELL was materially unfortunate in having lived in a region where his knowledge of systematic botany yielded him no financial remuneration, save from the limited sale of his book. His love of study and enjoyment of the vastness of the Pacific Northwest he considered ample reward. The sad part of his later life was his limited finances. For the last several years he was compelled to live in a poor foreign section of Portland, eking out a frugal existence in a small grocery-confectionery store, which also served as his residence. When visited last by the writer, he was making coarse teamsters mittens on a sewing

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machine for seven cents a pair. Under such conditions was his book revised. Mr. HOWELL, however, was very cheerful at all times and betrayed no impatience with depressing external conditions.

According to his own statement, the picture here produced is the only one ever taken of him. It represents him seated at his typewriter with the first copy of his revised flora. Behind him are seen stacks of completed mittens. It was made by the writer during a visit, October 14, 1910.—HURON H. SMITH, *Field Museum of Natural History, Chicago.*

THE SEEDLING OF PHYLLOCARPUS

(WITH ONE FIGURE)

When recently collecting insects at Gualan, Guatemala, Mrs. COCKERELL was so fortunate as to discover a new species of *Phyllocarpus*, a genus previously known from a single species found in Brazil. It is a large tree, with magnificent red flowers, much visited by insects. The circumstances attending the discovery have been related at some length in the *Canadian Entomologist* (September 1912, pp. 278, 279). Seeds were later obtained by Mr. E. MORRIS, and we were successful in getting some of them to germinate. I described the seedling in an early stage, before the fleshy cotyledons had appeared, and was away from home during the development of the later stages. From the accompanying figures it will be seen that the seedling is essentially like that of *Caesalpinia*. At the stage represented by the figures, the following characters are apparent:

FIG. 1.—Seedling of *Phyllocarpus*, n. sp.: from Gualan, Guatemala, by W. P. COCKERELL; apical leaflet not expanded.

Epicotylar stalk strongly pubescent, with spreading fine hairs as long as half its diameter, and more abundant short curled ones; petioles the same, only more hairy; first leaves 7-foliolate; leaflets light pea green, rather broad lanceolate, quite entire, nearly sessile, but inequilateral at base; perfectly glabrous except the margins, which are densely white-hairy, and the midribs beneath, which are hairy like the petioles.—T. D. A. COCKERELL, *University of Colorado, Boulder.*

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CURRENT LITERATURE

MINOR NOTICES

A new color guide.—A new color guide by Dr. ROBERT RIDGWAY,[1] the well known ornithologist, is practically an entirely revised and much enlarged edition of his earlier nomenclature of colors (1886) with 17 plates and 186 colors as against 53 plates and 1115 colors in the present work. The color work was done by A. Hoen & Co., Baltimore, and is much more uniform in different copies than in the earlier edition, which was hand-stenciled from several mixings of the same color; while in the present work each color for the whole edition of 5000 copies was prepared from one lot of color and uniformly coated at one time.

The work is designed to be equally useful to botanists, florists, artists, dyers, merchants, and chemists who require a standard color scheme. The colors have evidently been standardized to a degree of accuracy not hitherto attained in any color chart. The colors are one-half by one inch, arranged on a heavy gray paper in three vertical columns of 7 colors each. All the colors are named as well as symbolized, but if a given color comes between "hermosa pink" (1 *f*) and "eosine pink" (1 *d*), it could be designated 1 *e*. In this manner about 2385 additional colors or a total of 3500 can be designated. Undoubtedly exception will be taken to some of the names, but in this the personal equation plays such a large part that decisions must be rather arbitrarily rendered. The primary colors have been standardized by Dr. P. G. NUTTING of the U.S. Bureau of Standards.

A table of percentages of color, together with an explanation of the amount of white, black, or neutral gray used as above, will give an approximately ready clue to the reproduction of any color in the guide, the only uncertain factor being the possible lack of standardized primary colors to begin with. Definitions of the principal color terms, such as color, shade, tint, hue, tone, etc., which are used almost interchangeably by many people, will repay careful study by those not familiar with their exact use.

A slight error on p. 12, due to a misunderstanding, should be corrected. Mr. F. A. WALPOLE had no connection with the color project of the American Mycological Society, the preparation of which was delegated to the late Dr. L. M. UNDERWOOD, Dr. W. A. MURRILL, and the writer. MR. WALPOLE died before the committee was appointed, and the project was abandoned after two years' work by the committee in favor of Dr. RIDGWAY'S work which had not previously come to their notice.—P. L. RICKER.

[1] RIDGWAY, ROBERT, Color standards and color nomenclature. pp. 44. *pls.* 53. Published by the author (3447 Oakwood Terrace N.W., Washington, D.C.). 1912. $8.00.

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Homologizing plants and insects.—In attempting to homologize the various parts of plants and insects, JANET[2] has succeeded in proposing several additions to our already overloaded vocabulary. The sporangium of *Marchantia* contains "isogynospores" and "isoandrospores," while that of *Selaginella* contains "macrogynospores" and "macroandrospores." The vocabulary consists mostly of words like these, which are easily understood but unnecessary and not at all likely to become a permanent part of our burden. The plant ("orthophyte") consists of a gametophyte, beginning with the spore and ending with the "gynogametes" and "androgametes," and a sporophyte, beginning with the zygote and probably including the rest of the life history, although the table gives the sporangium (called the "gynosporangium" and "androsporangium" in *Selaginella*, and the nucellus and pollen sac in spermatophytes) as the final member of this generation.

The insect is an "orthozoite," consisting of a "gametozoite" and a "sporozoite" generation. The gametozoite generation begins with a generative cell (cellule génitale) which produce "gonads," gametangia, and finally "gynogametes" and "androgametes." The sporozoite generation begins with the fertilized or parthenogenetic egg, and includes the rest of the life history.

Several years ago the reviewer tried to show[3] that, in animals as in plants, generations are characterized by the haploid and diploid number of chromosomes. JANET's paper is based upon current knowledge rather than upon any new evidence. However, we agree with him, or rather he agrees with us, that there is an alternation of generations in animals.—CHARLES J. CHAMBERLAIN.

Flora of New Guinea.—Another volume of the botanical results of the Dutch scientific expedition to New Guinea (1907 and 1909) under the auspices of Dr. H. A. LORENTZ has now appeared.[4] The first part of the botanical report was reviewed in this journal.[5] The collaborators are as follows: S. H. KOORDERS, L. RADLKOFER, A. PULLE, J. VALCKENIER SURINGAR, E. ROSENSTOCK, MAX FLEISCHER, TH. VALETON, J. J. SMITH, A. ENGLER and K. KRAUSE, C. LAUTERBACH, J. PERKINS, and L. DIELS, 72 families and 292 genera being represented, including 599 species, 153 of which are new. Three new genera are published as follows: *Capitularia* (Cyperaceae), *Gjellerupia* (Opiliaceae), and *Nouhuysia* (Guttiferae). Most of the families are introduced merely to

[2] JANET, CHARLES, Le sporophyte et le gamétophyte du végétal; le soma et le germen de l'insecte. 8vo. pp. 65. Limoges: Ducourtieux et Goût. 1912.

[3] CHAMBERLAIN, CHARLES J., Alternation of generations in animals, from a botanical standpoint. BOT. GAZ. 39:137–144. 1905.

[4] Nova Guinea. Résultats de l'expedition scientifique Néerlandaise à la Nouvelle-Guinée, en 1907 et 1909, sous les auspices du Dr. H. A. LORENTZ. Vol. VIII. Botanique. Livraison IV. 4to. pp. 613–898. *pls. 113–159.* Leide: E. J. Brill. 1912. Fr. 27. 50.

[5] BOT. GAZ. 49:464. 1910.

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include some additional species, but the Cyperaceae (19 genera and 97 species, 6 of which are new), Rubiaceae (16 genera and 36 species, 11 of which are new), and Filices (39 genera and 86 species, 18 of which are new) are presented with a measure of completeness. Aside from these families, the largest additions of new species are to Ericaceae (14), Euphorbiaceae (12), and Musci (10).—J. M. C.

Paleobotanical literature.—The third volume of JONGMAN'S *Die palaeobotanische Literatur* has appeared,[6] including the bibliography of 1910 and 1911. The great usefulness of this publication needs no explanation, and now that paleobotany has come to be an essential part of the morphology of vascular plants, it will serve a much larger group of botanists than the title once would have indicated. The list of authors (40 pp.) includes 374 names, representing 762 titles. The list of literature is admirably organized, so that almost any clue can be followed to the literature of a subject.—J. M. C.

NOTES FOR STUDENTS

The mucors.—Prominent among recent publications on the Mucoraceae are two papers by HAGEM[7] which deal with the distribution, taxonomy, and physiology of the soil-inhabiting mucors occurring in the vicinity of Christiania, Norway. A systematic search has revealed the presence in the soil of an unsuspected wealth and variety of these organisms, strangely in contrast with the rarity of their spores in the atmosphere. In the first paper, which deals with taxonomy and distribution, 20 species are described. Of these, 16, including 7 new species, were isolated from cultivated and forest soils. Most of these were isolated many times and some were present in remarkable abundance. Among the most frequently encountered species, *Mucor racemosus*, *M. hiemalis*, and *M. nodosus* are abundant in cultivated lands; *M. Romannianus* is most frequent in coniferous forests (50,000 spores per gram of soil), but *M. strictus*, *M. flavus*, and *M. sylvaticus* are also common. Some forms like *M. racemosus*, *M. hiemalis*, *Absidia Orchidis*, and *Zygorynchus Moelleri* are widely distributed both in cultivation and in forest soils. As showing the rarity of the spores of mucors in the air, only 8 species were isolated by means of Petri dishes containing culture media, and exposed for periods of 1–2 hours both in town and country.

The second paper deals chiefly with problems of nutrition. A large number of compounds were tested with respect to their availability as sources of

[6] JONGMANS, W. J., Die palaeobotanische Literatur. Bibliographische Übersicht über die Arbeiten aus dem Gebiete der Palaeobotanik. Dritter Band. Die Erscheinungen der Jahre 1910 und 1911 und Nachträge für 1909. pp. 569. Jena: Gustav Fischer. 1913. *M* 26.

[7] HAGEM, O., Untersuchungen über norwegische Mucorineen. I. Vidensk. Selsk. Skrift. no. 7. pp. 50. *figs. 22.* 1907; *ibid.* II. no. 4. pp. 152. 1910.

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nitrogen and of carbon for the mucors. The mass of detail is too great and too diverse to permit of recapitulation; the main features of the results, however, may be briefly summarized. The 23 mucors studied fall into two clearly separated groups with respect to their ability to assimilate nitrogen from nitrates and nitrites. In relation to these compounds it is interesting to note that all forms which were capable of assimilating nitrates were also capable of assimilating nitrites. As with other plants, the nitrates are reduced to nitrites and these to ammonia in the process of assimilation. All forms grew well when nitrogen was supplied in the form of ammonium salts. On urea, 18 species thrived, but *Mucor Romannianus* failed. In cultures with urea, ammonium carbonate is formed. Acetamide is not utilized. Uric acid is only slightly soluble, but gives good growth. The amino-acids have little nutrient value when they are the sole source of both carbon and nitrogen. When carbon is supplied in the form of glucose, the amino-acids, especially leucine and tyrosine, are utilized as a source of nitrogen by many of the soil mucors. In all cases ammonia accumulates in the culture medium. Of the non-nitrogenous carbon compounds, mannite and glycerin are not used when ammonium sulphate is the only source of nitrogen; with potassium nitrate, however, these polyatomic alcohols are assimilated by 3 or 4 species. With the exception of maltose, the disaccharides are not used except in a few cases. Six species grew well on saccharose, but of these only two showed the accumulation of reducing sugar in the culture fluid. The species which thrive on saccharose are unable to utilize that sugar when amino-acids serve as the only source of nitrogen. In explanation the author suggests that the action of the invertase of the fungi is inhibited by the presence of ammonia split off from the amino-acids. Starch in general seems not to be utilized, a fact which is all the more interesting since the conversion of starch into glucose by some species of *Rhizopus* is the basis of a commercial process. Few species grow on inulin and pectin, but some on xylan and cellulose. Of the glucosides, helicin and salicin were tried. Helicin proved valueless, while a number of mucors were capable of utilizing salicin, but only to a limited extent because of the toxic properties of the decomposition products formed.

These results on the whole seem to indicate that most of the common substances which reach the soil from the plant are only poorly suited for the nutrition of a group constituting, according to these investigations with the exception of the bacteria, one of the most abundantly represented classes of soil-organisms. It would be an interesting problem to determine to what extent the nutrition of soil mucors is dependent upon decomposition of plant products brought about by bacteria and other soil organisms.

In a third paper,[8] which forms the conclusion of HAGEM's investigations of Norwegian mucors, the author gives critical notes on their nutrition. *Mucor*

[8] HAGEM, O., Neue Untersuchungen über norwegische Mucorineen. Ann. Myc. 8:265–286. *figs. 11.* 1910.

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saturninus, *M. christianiensis*, *M. dispersus*, and *M. corticolus* are described as new in this paper. *M. norwegicus* Hagem, which was described as new in the first paper, is here regarded as a synonym of *M.* (*Rhizopus*) *nodosus* (Namyslowski) Hagem.

NAMYSLOWSKI[9] describes a new species of *Zygorynchus* isolated from the soil. This species, like the other species of the genus (*Z. Moellerii* and *Z. heterogamus*), is monoecious.

In another paper,[10] NAMYSLOWSKI has reported a long series of experiments in which, after the fashion of KLEBS, he attempts to determine the influence of various food substances in different concentration on the production of zygospores and sporangia by the mucors. The data do not allow of either general or precise conclusions, but show that the kind and concentration of nutrients have a not very well defined influence in determining the relative abundance of zygospores and sporangia. The work further brings out the fact that the distinction between monoecious and dioecious species is not always sharp, for some of the monoecious forms, like *Zygorynchus*, produce zygospores along the line of contact between two adjoining colonies, and some dioecious species show a tendency to form zygospores on mycelia derived from single spores. In one case, *Absidia glauca*, the author even succeeded in isolating a monoecious race from a species which is usually considered to be dioecious.

A number of short papers by different authors treat of the formation of zygospores and of nuclear phenomena in the mucors. LENDNER[11] has examined the method of origin of the zygospore in a number of mucors representing both monoecious and dioecious species. His observations go to show that the gametangia originate at points where two branches of the mycelium accidentally come into contact, and not, as is usually stated, on branches which grow toward each other as the result of some sort of a stimulus. MOREAU,[12] who has studied nuclear phenomena in the hyphae and zygospores of several mucors, reports that the divisions in the hyphae and gametangia are normally mitotic and simultaneous. In the columella of *Rhizopus* amitotic divisions, which

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[9] NAMYSLOWSKI, B., *Zygorynchus Vuilleminii*, une nouvelle mucorinée isolée du sol et cultivée. Ann. Myc. **8**:153–155. *figs. 9.* 1910.

[10] NAMYSLOWSKI, B., Studien über Mucorineen. Bull. Intern. Acad. Sci. Cracovie. Ser. B. 1910:577–519. *figs. 2.*

[11] LENDNER, A., Observationes sur les zygospores des Mucorinées. Bull. Soc. Bot. Genève. II. **2**:56–59. *figs. 4.* 1910.

[12] MOREAU, F., Première note sur les Mucorinées, le noyau au repos.—Le noyau en division: mitose et amitose. Bull. Soc. Mycol. France **27**:204–210. *figs. 12.* 1911.

———, Deuxième note sur les Mucorinées.—Fusions de noyaux et dégénérescence nucléaire dans la zygospore.—Fusions de noyaux sans signification sexuelle. *Ibid.* 334–341. *figs. 4.*

———, Les phénomènes internes de la reproduction sexuelle chez quelques Mucorinées hétérogames. Bull. Soc. Bot. France **58**:618–623. *figs. 4.* 1911.

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apparently indicated degeneration, were observed. In the zygospores he finds that multiple fusion with degeneration of the supernumerary nuclei takes place. The fusion is preceded by a division. *Zygorynchus* offers a variation from other forms in the fewness of the nuclei which fuse (4 in one species) and in the tardiness of the fusion.

The process of zygospore formation in *Zygorynchus*, according to GRUBER,[13] shows some peculiarities which have not been observed in mucors heretofore. The zygospore arises at the point of contact between the terminal portion of an erect hypha and a lateral branch arising from the same hypha or rarely from a different hypha. At the point of contact the gametangia grow out from each hypha. Only the female gametangium is cut off by a wall at its base from the parent cell. Later a partly formed wall arises midway between the base and apex in the female gametangium, but this wall is rarely completed and soon disappears. The male gametangium remains in connection with the parent hypha. After the fusion of the gametangium a differentiated portion of the protoplasm of the male gametangium passes into the female gametangium, carrying with it 20–30 nuclei. The fusion of nuclei was not observed on account of their minuteness. The author believes that a multiple fusion takes place and that subsequently the fused nuclei divide to give the large number subsequently found in the zygote. He does not note the reduction in number observed by MOREAU. The resemblance of the manner of formation of the zygospore in this form to that of oospores suggests that *Zygorynchus*, which in other characteristics corresponds with the mucors, is akin to the oomycetes.—H. HASSELBRING.

Cecidology.—A very interesting and valuable contribution is a study of a citrus tree cecidium caused by *Sphaeropsis tumefaciens* Hedges by HEDGES and TENNY.[14] The organism was first isolated from lime tree knots from Jamaica in 1904. The knots vary in size from ¾ to 3 inches, and are usually more or less spherical; they are light in color and smooth when young but become black and furrowed with age. The interior of the knot is hard and compact, while the outer part is soft and crumbling in character. They are frequently more or less covered with typical witches-broom growths. They occur on both old and young growths and at any season of the year, and eventually cause the death of the plant. The mycelium may grow in any tissue, but is confined to the intercellular spaces, but unfortunately the authors have not given a discussion of the structural characters of the malformations. The fungus penetrates the wood for considerable distances beyond the point of inoculation, thus making pruning an unsatisfactory treatment. Pycnidia

[13] GRUBER, E., Einige Beobachtungen über den Befruchtungsvergang bei *Zygorynchus Moelleri* Vuill. Ber. Deutsch. Bot. Gesells. 30:126–133. *pl. 1.* 1912.

[14] HEDGES, FLORENCE, and TENNY, L. S., A knot of citrus trees caused by *Sphaeropsis tumefaciens*. Bull. no. 247. U.S. Dept. Agric. Bur. Pl. Industry. 1912.

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may or may not be produced; spermogonia are produced, but perithecia and conidia have not been observed.

Another important contribution to our knowledge of American cecidology comes from COSENS,[15] of the University of Toronto. After a brief review of our present knowledge of cecidology, he discusses the results of his own investigations. The subdivisions are arranged with reference to the insects causing the galls, but the discussions are primarily botanical in character. The results of these studies confirm much of our previous knowledge and make valuable additions. The *Eriophyes* galls show a well defined series from simple indentations to well developed pouches, and from modifications of epidermis only to the palisade and mesophyll also. The modifications are those of degree rather than of kind. In the hemipterous galls the stimulation is from one side and is disseminated equally in all directions. The lepidopterous galls are characterized as a simple type. The glands are larger than in the normal tissues. The dipterous galls are extremely variable in degree of complexity and the glands are very abundant. The sawfly galls of the Hymenoptera show a great proliferation of tissue, with but very little differentiation. Tannin was especially abundant in the epidermis and bast and probably serves for the protection of the larvae. Other members of this order produce the most highly developed galls with very complicated structures. Probably the most vital part of this paper is the series of physiochemical experiments with the larvae, in which the author found that the larvae "secrete an enzyme, capable of changing starch to sugar, which acts on the starchy constituents of the nutritive zone and accelerates the rate of their change to sugar. The material thus prepared supplies nourishment for both the larva and the gall. The protoplasm of the latter is thus rendered unusually active, since it receives an abnormal quantity of available food material in a limited area. The hypertrophy and cell proliferation and probably also the appearance of vestigial tissue or other primary characters are the response of the protoplasm of the host to the additional food supply." The author also says that it is not necessary in all cases for the stimulus to be applied to the cambium, but that it may be applied to any actively growing tissue; that this stimulus acts on tissues at considerable distance from the point of application; that certain inquilines have the power of gall production to some extent.

A very brief paper on pistillody by LEWIS[16] shows the necessity for botanists to give more attention to the recording of the abnormal structures in plants. In this case both the anther and the filament were inflated and bore ovules, the anther being modified into a sessile leaflike structure with a stigmatose edge.

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[15] COSENS, A., A contribution to the morphology and biology of insect galls. Trans. Canadian Inst. 11:297–387. *pls. 13.* 1912.

[16] LEWIS, I. W., Pistillody in *Argemone platyceras* Link and Otto. Torreya 12:85–88. 1912.

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Among the important foreign papers which are of some interest to botanists are the following: Two systematic papers by HOUARD[17] in which the author gives descriptions and notes based on the characters of the galls. Docters VAN LEEUWEN-REIJNVAAN[18] continue their very valuable descriptions of the galls of Java, describing 99 species. These descriptions are purely botanical and in most cases the species is not named, but is placed in such genus or family as may be indicated by the external characters of the cecidium. This is therefore merely the record and description of certain types of cecidia found on certain species of plants and becomes an important starting-point for future workers.—MEL T. COOK.

Motile isogametes in the Chytridiales.—KUSANO[19] has demonstrated in *Olpidium Viciae*, a new species parasitic on *Vicia unijuga*, that the free swimming zoospores sometimes conjugate much as in the lower green algae. Similar copulation was reported many years ago by FISCH in *Reesia*, which is closely related to *Olpidium*, but his account has not been generally accepted. KUSANO, however, not only followed the zygote to infection, but traced its cytological history through to the next generation of zoospores. Conjugation, which seems to occur only during the amoeboid intervals between active swarming, appears to be induced by a contact stimulus. There is a slight physiological differentiation among the zoospores in that not all of those which come together appear to have a sexual affinity, although one of such a mismated pair may often fuse with a third which comes into contact with them. Zoospores from old sporangia which have been prevented from discharging by lack of water copulate more freely than those which have recently matured. Conjugated or unconjugated zoospores may infect the host, one giving rise to resting spores, the other to zoosporangia. After encysting on the outside of the host, the young parasite penetrates the cell wall and escapes into the cell, where it is freely carried around by the rotation of the host cytoplasm, until it finally comes to rest near the nucleus. Though naked until nearly mature, it never undergoes amoeboid deformation as in *Reesia* and *Monochytrium*. The zoospores are discharged through very short wartlike exit beaks, of which four or five may develop on a single sporangium, though only one functions.

In its cytology this organism is so similar to *Monochytrium* as to make it evident that the two are very closely related, although in the latter the spores

[17] HOUARD, C., Les collections cécidologiques du laboratoire d'entologie du Museum d'Histoire Naturelle de Paris: l'herbier du Dr. Fairmaire. Marcellia 11:11–46. 1912; and Galles de Mayr et Muller. Marcellia 11:107–114. 1912.

[18] VAN LEEUWEN-REIJNVAAN, W. DOCTERS and J., Einige gallen aus Java. VI. Marcellia 11:49–100. 1912.

[19] KUSANO, S., On the life history and cytology of a new *Olpidium* with special reference to the copulation of motile isogametes. Jour. Coll. Agric. Tokyo 4:141–199. *pls. 15–17. fig. 1.* 1912.

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do not conjugate until after infection. The nuclei of the zoosporangium divide during the growth stages by a process of amitosis like that figured by the writer in *Monochytrium*, but in the later reproductive stages they divide by mitosis, recalling conditions in *Synchytrium* and *Chrysophlyctis*. Fusion of the gametic nuclei in the zygote is delayed until the spring of the following year, the resting spores having of course matured in the meantime. Before they conjugate, however, they undergo a very peculiar process of budding by which large amounts of chromatin are extruded into the cytoplasm and central vacuole. The first division of the fusion nucleus appears to represent reduction, after which the nuclei are multiplied rapidly until the old resting spore becomes a zoosporangium very similar to the temporary sporangia.

The demonstration of such a primitive type of sexuality in *Olpidium* would seem to indicate clearly that it and its allies cannot be considered as having degenerated from higher fungi under "the debasing influence of parasitism." On the other hand, the facts so far brought to light do not give a clear indication of the source from which these forms may have come. It is evident, however, that they are polyenergid in contrast with *Synchytrium*, *Woroninella*, and *Chrysophlyctis*, which are essentially monoenergid, becoming coenocytic only during the reproductive period. KUSANO points out that this fact rules out the monoenergid Endosphaeraceae as indicative of the line of descent of *Olpidium*, though not necessarily eliminating the lower Protococcoideae in the region of *Chlamydomonas*. Now that cytological studies of the Archimycetes are beginning to accumulate, it is becoming increasingly evident that they represent not a single phylum, but a conglomeration of heterogeneous forms which have little in common except their apparent simplicity.—ROBERT F. GRIGGS.

Physiological effect of Bordeaux mixture.—Aside from its fungicidal value, Bordeaux mixture has been reported by several investigators to have a physiological action which results in an increased assimilatory activity of sprayed plants. This action has been further investigated by EWERT, who in a former paper reported experiments which indicate that, contrary to the generally accepted opinion, the physiological effect of Bordeaux mixture on the leaves of plants is detrimental. In the present paper EWERT[20] reports the results of an investigation of the effects of Bordeaux mixture on the assimilatory activity of the potato, radish, and bean; and on the sugar content of currants. The experiments with potatoes, radishes, and beans were conducted with plants grown in tanks under controlled conditions, and in soil kept at a constant water content. It was found that almost without exception the yield of tubers, roots, and pods, and of total dry matter was depressed by a covering of

[20] EWERT, R., Weitere Studien über die physiologische und fungicide Wirkung der Kupferbrühen bei krautigen Gewächsen und der Johannisbeere. Zeitschr. Pflanzenkrank. 22:257–285. 1912.

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Bordeaux mixture on the leaves. The depression of the yield increased with the strength of the mixture applied. As a rule, the beneficial effect of the mixture has been ascribed to the shade-effect of the covering, which was supposed to protect the plants from too great an intensity of light. EWERT found that bean plants shaded by a light gauze during periods of greatest illumination gave a greater yield and retained their leaves longer than unshaded plants. A similar effect produced by a covering of Bordeaux mixture, he thinks, would be counterbalanced by the ill effects of the shade on cloudy days and the toxic effects of the copper. In the experiments with currants, it was found that spraying berries with Bordeaux mixture or dipping them into it increased their sugar content considerably. How this effect is brought about is not yet clear. This effect on the berries is so striking that a decrease in their sugar content, due to depression of the assimilatory activity resulting from spraying the leaves, can be easily overlooked. Two sprayings of the leaves with 4 per cent mixture resulted only in a decrease of 0.5 per cent in the sugar content of the berries which were protected from the spray. This decrease is attributed to the deleterious effects of the mixture on the assimilatory activity of the leaves.—H. HASSELBRING.

Dispersal of seeds by ants.—SERNANDER[21] organized the disjointed and inaccurate data on the importance of ants in the distribution of certain seeds and fruits, and added a wealth of observations and experimental evidence upon this phase of ecological science. This particular kind of distribution he termed "myrmecochorous," and showed that it was almost wholly due, not to the supposed mimicry of the pupa of ants by the seeds, but to the presence of certain oil bodies or "elaiosomes" which serve as food for the ants and hence cause their collection and storage. These bodies occur as various morphological modifications or appendages of seeds and fruits, various types being distinguished. Some 120 plants were at that time listed as myrmecochorous, and evidence was produced that the activity by a single colony of ants for one season includes the transportation of many thousand seeds, some to distances of 15 to 70 meters.

A recent article by MORTON[22] calls attention to the important foundation laid by SERNANDER, cites the contributions that have appeared since that date, and summarizes the present situation of myrmecochory. The number of myrmecochorous plants has been considerably increased, although these studies have been almost exclusively confined to Europe. The associations affected are mostly those of woodland and ruderal plants. MORTON concludes that ants have been acting as a selection factor for such plants at least since

[21] SERNANDER, R., Entwurf einer Monographie der europäischen Myrmekochoren. Kungl. Vetensk. Akad. Upsala 41: 1906.

[22] MORTON, FRIEDRICH, Die Bedeutung der Ameisen für die Verbreitung der Pflanzensamen. Mitt. Naturwiss. Vereins 1912:77–112. Reprint by author, 1913.

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the Tertiary age, and that the center of distribution of woodland forms has been the forests of central Europe, while ruderal myrmecochorous forms have radiated from the Mediterranean region. The elaiosomes, in his opinion, have originated in many ways quite independently of the purpose they now serve as factors in distribution.—GEO. D. FULLER.

Anisophylly.—In *Strobilanthes anisophyllus* FIGDOR,[23] experimenting to discover the cause of the development of isophyllous shoots, is satisfied that it is a reversion to juvenile form because seedlings show no anisophylly until they have attained considerable size, and he thinks that it should be possible to prolong isophyllous development indefinitely. He agrees with BOSHART[24] that good nutrition tends to promote isophylly, but takes exception to his statement that anisophylly is to be explained through dorsiventrality. BOSHART[25] in a more recent paper lays emphasis on his former points, such as the asymmetry of the growing point of anisophyllous shoots and the very slight effect of gravity and light. He thinks that the latter factor may affect anisophylly through increasing or decreasing the vigor of the shoot, the weakening favoring asymmetry. He finds, on the contrary, light exercising a direct influence upon the anisophylly of certain species of *Selaginella* and *Lycopodium*.

Anisophyllous rosettes in various species of *Sempervivum* have been experimentally shown by DOPOSCHEG-UHLÁR[26] to result from an inclination of the stem axis toward the horizontal, but whether the response was effected by gravity or light he was unable to determine. The anisophylly seems to disappear toward the close of the growing season and to be renewed early the following spring. The phenomenon in nature is closely associated with the crowded grouping of young plants about the parent rosette in the characteristic multiplication by offshoots.—GEO. D. FULLER.

Morphology of Agathis.—EAMES[27] has investigated the Kauri, the famous timber tree of the Australasian region. Our knowledge of the morphology of the araucarians has lagged behind that of the other coniferous tribes, so that this contribution is very timely. An outline of the results is as follows. Pollination occurs a year after the appearance of the ovulate strobili, and fertiliza-

[23] FIGDOR, W., Das Anisophyllie-Phaenomen bei Vertretern des Genus *Strobilanthes* Blume. Ber. Deutsch. Bot. Gesells. **29**:549–558. 1911.

[24] BOSHART, K., Beiträge zur Kenntnis der Blattasymmetrie und Exotrophie. Flora **103**:91–124. 1911.

[25] BOSHART, K., Über die Frage der Anisophyllie. Ber. Deutsch. Bot. Gesells. **30**:27–33. 1912.

[26] DOPOSCHEG-UHLÁR, J., Die Anisophyllie bei *Sempervivum*. Flora **105**:162–183. 1913.

[27] EAMES, ARTHUR J., The morphology of *Agathis australis*. Ann. Botany **27**:1–38. *figs. 92. pls. 1–4.* 1913.

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tion 13 months after pollination. The numerous archegonia are scattered over the broader micropylar portion of the gametophyte. The pollen grains germinate in the axils of the cone scales, before there is any differentiation of a micropyle. The pollen tubes are long and branching and penetrate the cone axis, and also the phloem and even the xylem of the scale traces. The two sperms are somewhat unequal cells with delicate walls, and their nuclei are as large as the egg nucleus. The proembryo is three-tiered, the uppermost tier forming the suspensor, the middle tier the embryo, and the lowest tier a protective cap. The cone scale is said to be structurally double, representing a combination of the bract and scale in Abietineae. It is concluded that the araucarians represent a highly specialized branch of the Coniferales, and that *Araucaria* is probably more ancient than *Agathis*.—J. M. C.

Anatomy of Botrychioxylon.—SCOTT[28] has described in detail the anatomy of *Botrychioxylon*, one of the paleozoic Zygopterideae. As in all the members of this family, a true pith is absent, the primary wood of the stele being intermixed with much parenchyma. Around the whole primary cylinder, as well as around the diarch leaf-trace, is a wide zone of secondary wood, a condition rare or absent in most of the family. The petiolar bundle resembles somewhat that of *Dineuron* or *Metaclepsydropsis*. Because of the unusual development of secondary wood, *Botrychioxylon* is considered by its author to approach the living *Botrychium* more closely than has any previously described form, and to present evidence for the affinity of the Zygopterideae and Ophioglossaceae. This conclusion is in harmony with that general theory, now the subject of much dispute, which derives the true pith of modern ferns from tissue which was primitively stelar.—E. W. SINNOTT.

Fertilization in Gagea.—In *Gagea lutea*[29] the usual double fertilization is the rule, but occasionally both male nuclei fuse with the egg. Another apparently unusual feature is the inclusion of cytoplasm between the fusing nuclei both during the fertilization of the egg and during the fusion of the polar nuclei. The included cytoplasm soon disorganizes. This is the second record of such a cytoplasmic inclusion, the first having been made by BROWN[30] in his study of *Peperomia*. The dispermic fertilization and a study of the literature of chromosome numbers leads NĚMEC into speculations upon the origin of mutation.—CHARLES J. CHAMBERLAIN.

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[28] SCOTT, D. H., On *Botrychioxylon paradoxum*, sp. nov., a paleozoic fern with secondary wood. Trans. Linn. Soc. Bot. 7:373–389. *pls. 37–41.* 1912.

[29] NĚMEC, B., Über die Befruchtung bei *Gagea*. Bull. Internat. Acad. Sci. Bohême 1912:1–17. *figs. 19.*

[30] BROWN, W. H., The exchange of material between nucleus and cytoplasm in *Peperomia sintenisii*. BOT. GAZ. 49:189–194. *pl. 13.* 1910.

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GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

A

Acaena 92
Acarospora cervina 394; chlorophana 394; **thamnina** 395; **thermophila** 394
Acids, toxic 409
After ripening 287
Agaricaceae 332
Agathis, morphology of 471
Agave 332
Algae 94
Allomyces arbuscula 92
Alnus, root tubercles of 254
Amelanchier 333
Ames, Adeline 397
Ames, O., work of 92
Andrews, F. M., work of 331
Angiopteris, vegetative reproduction in 262
Angiosperms, earliest European 335
Anisophylly 471
Ants, dispersal of seeds by 470
Aptiana 335
Arabis Menziesii **lata** 374; Menziesii **lanuginosa** 374; pedicellata 374
Araceae 94
Araucaria brasiliensis, morphology of 97
Araucarians, evolution of 172
Araucarioxylon 335
Arber, E. A. Newell, "The natural history of coal" 170
Arctostaphylos **cratericola** 437
Asagraea spinosa 312
Ascobolus 331
Asymmetry, cause of leaf 407
Atmometers, revolving table for standardizing 249; standardizing 263

B

Balls, W. Lawrence, "Cotton plant in Egypt" 329
Basanacantha **grandifolia** 436
Baylesia 94
Bayliss, Jessie S., work of 176
Beccari, O., work of 92
Begonia 94
Berridge, Emily M., work of 171, 172
Bertrand, G., work of 88, 89, 90
Besa 94
Bissell, C. H., work of 92
Bitter, G., work of 92
Black spruce, layering in 452
Blake, S. F., work of 92
Blastenia ferrugeina 396
Bog waters, effect of on root hairs 314
Bolelia brachyantha 382
Bordeaux mixture, physiological effect of 469
Boshart, K., work of 407, 471
Botrychioxylon, anatomy of 472
Botryopterideae 263
Bottomly, W. B., work of 255
Bower, F. O. 384
Brachyoxylon 335
Brainerd, E., work of 92
Brand, A., work of 92
Brandegee, T. S., work of 92
Brauns, H., work of 92
Brenner, W., work of 90
Broadhurst, J., work of 92
Brown, Nellie E., work of 257
Brown rots, winter condition of 95
Brown, W. H., work of 472
Bryosedgwickia 93
Burlingame, L. Lancelot 97
Burtt-Davy, J., work of 92
Butler, E. J., work of 92
Butters, F. K., "Minnesota trees and shrubs" 330

C

Calceolaria 332
Calcium-magnesium ratio 96
Caloplaca elegans 396; murorum 396
Calyptrella **cycliophylla** 434
Candelariella cerinella 396
Candelspora 332
Capitularia 462
Carex 93
Caryocar **costaricense** 431

Digitized by Google

Castilleja 93; **Bennittii** 380; **curticalix** 380; fasciculata **inverta** 381; miniata 379; rhexifolia **pubens** 380
Cave, G. H., work of 332
Cecidology 466
Cedar, habitats of the red 264
Central America, orchids of 332; undescribed plants from 431
Cereus 333
Chalazogams, evolution of 94
Chamberlain, Charles J. 94, 141, 254, 262, 403, 462, 472; work of 462
China, plants of 94
Chytridiales, motile isogametes in 468
Citrus trees, knot diseases of 407
Claassen, E., work of 92
Clematis aurea 373
Clements, F. E., "Minnesota trees and shrubs" 330
Clibadium 332
Climax forest of Isle Royale 1, 115, 189
Clintonia corymbosa 382
Coal, natural history of 170
Cockerell, T. D. A. 460
Collins, G. N., work of 261, 404
Collins, J. Franklin, "Keys to trees" 330, 402
Collins, T. S., work of 93
Conard, H. S. 80
Coniferales, ray tracheids in 56
Contributors: Ames, Adeline 397; Bower, F. O. 384; Burlingame, L. L. 97; Chamberlain, C. J. 94, 141, 254, 262, 403, 462, 472; Cockerell, T. D. A. 460; Conard, H. S. 80; Cook, M. T. 468; Cooley, J. S. 421; Cooper, W. S. 1, 115, 189; Coulter, J. M. 171, 172, 259, 260, 261, 262, 263, 264, 330, 336, 402, 462, 463, 471; Cowles, H. C. 328, 407; Crocker, Wm. 167, 253, 337; East, E. M. 177, 404, 405; Eckerson, Sophia 287; Fuller, G. D. 96, 175, 176, 253, 257, 258, 260, 263, 264, 328, 329, 334, 402, 408, 452, 470, 471; Givler, J. P. 400; Greenman, J. M. 92, 254, 331, 332, 402; Griggs, R. F. 468; Hasselbring, H. 92, 96, 254, 257, 463, 469; Hawkins, L. A. 265; Hemenway, A. F. 236; Herre, A. W. C. T. 392; Hoffman, C. 244; Holden, Ruth 56, 335; Jeffrey, E. C. 168, 170, 175; Knight, L. I. 337; Land, W. J. G. 439; Lipman, C. B. 409; Martin, J. N. 96, 174; Nelson, Aven 372; Nichols, G. E. 249; Osterhout, W. J. V. 446; Parish, S. B. 300; Petry, L. C. 155; Reed, H. S. 421; Ricker, P. L. 461; Rigg, G. B. 314; Sharp, L. W. 256, 258; Sinnott, E. W. 472; Smith, H. H. 458; Smith, J. D. 431; Snow, Laetitia M. 45; Starr, Anna M. 251; Sturgis, W. C. 400; Tower, W. L. 174; Transeau, E. N. 66; Wilson, F. H. 409; Yamanouchi, S. 74
Cook, Mel T. 468
Cooley, J. S. 421
Cooper, William S. 1, 115, 189; work of 96
Copeland, E. B., work of 93
Cordia **gualanensis** 438
Corydalis 93
Cosens, A., work of 467
Cotton plant 329
Coulter, John M. 171, 172, 259, 260, 261, 262, 263, 264, 330, 336, 402, 462, 463, 471
Cowles, Henry C. 328, 407
Craibiodendron 332
Crassulaceae, embryo sac of 258
Crocker, William 167, 253, 337
Crodelia 93
Crown-gall 257
Cyatheae 93
Cyperaceae 93, 463

D

Dalea *arborescens* 306; arborescens 313; *californica* 309; *Emoryi* 306; *Johnsonii* 308; *mollis* 302; *Parryi* 303; *polyadenia* 305; *Saundersii* 308; *Schottii* 309; *spinosa* 312
Darbishire, Otto V., work of 259
Darling, C. A., work of 331
Davidson, A., work of 331
Deam, Charles C., work of 331
DeFraine, E., work of 175, 261
Delaware Coast, plant associations of 45
Delphinium **megacarpum** 373
Diaporthe 93
Diastase, malt, effect of chlorides on 265
Dichothrix 333
Dicotyledons, phloem of 236
Didymosporangium repens 94
Diels, L., work of 462
Dingler, H., work of 334
Dioecism in Epigaea 256
Diplasiolejeunea 93
Discosiella 333
Dixon, H. N., work of 93
Dodge, B. O., work of 331
Doposcheg-Uhlar, J., work of 471
Downingia **brachyantha** 382; corymbosa 382
Dox, A. W., work of 91
Drainage, cold air 263
Drummond, J. R., work of 332

Digitized by Google

E

Eames, Arthur J., work of 471
East, E. M. 177, 404, 405
Echinocactus 332
Echinocereus 333
Eckerson, Sophia 287
Elmer, A. D. E., work of 93
Engler, A., work of 462
Ephedra 171; vegetative reproduction in 439
Epigaea, dioecism in 256
Epilobium 94
Ericaceae 463
Erigeron **elkoensis** 382; poliospermus **latus** 383
Eucalyptus 94
Euphorbiaceae 463
Eutypa gigaspora 94
Evans, A. W., work of 93
Ewert, R., work of 95, 469

F

Fairy ring fungi 176
Fawcett, H. S., work of 93
Fawcett, W., work of 93
Fedde, F., work of 93
Fern, a new Jurassic 264
Fernald, M. L., work of 92, 93
Field, E. C., work of 93
Figdor, W., work of 471
Filices 463
Finn, W., work of 94
Firth, R. H., work of 173
Fisher, M. L., work of 331
Fleischer, Max, work of 462
Forest Club Annual 176
Forest, climax, of Isle Royale 1, 115, 189
Frasera 331
Fuller, George D. 96, 175, 176, 253, 257, 258, 260, 263, 264, 328, 329, 334, 402, 408, 452, 470, 471
Fungi, fairy ring 176; metabolism of 85

G

Gagea, fertilization in 472
Gentiana affinis **major** 376
Geranium *atropurpureum* 376; caespitosum *gracile* 376; *furcatum* 376; *gracile* 376
Gibellula 333
Gilibertia **gonatopoda** 434; **stenocarpa** 435
Ginkgo, poisoning by 251
Givler, J. P. 400
Gjellerupia 462
Gloeotaenium, life history of 66
Glück, Hugo, "Wasser- und Sumpfgewächse" 328
Gnetales 172
Green algae 93
Greene, Edward Lee, "Carolus Linnaeus" 330
Greenman, J. M. 92, 254, 331, 332, 402
Griggs, Robert F. 468
Grimes, E. J., work of 331
Grüber, E., work of 466
Gymnosperms, recent work in 171
Gymnosporangium, effect on transpiration 421
Gyrophora reticulata 394; rugifera 394

H

Haberlandt, G., "Physiologische Pflanzenanatomie" 402
Hagem, O., work of 463
Hall, H. M., work of 93
Hamet, R., work of 93
Hapterophycus 94
Harper, R. M., work of 264
Harter, L. L., work of 93
Hartman, Max, "Protistenkerne" 254
Hasselbring, H. 92, 96, 254, 257, 463, 469
Haustorium of Striga 336
Hawkins, Lon A. 265
Hawley, H. C., work of 332
Hebonga 94
Hedges, F., work of 407, 466
Heimerl, A., work of 93
Heinricher, E., "Parasitischen Samenpflanzen" 252
Heller, A. A., work of 93, 332
Hemenway, Ansel F. 236
Hepaticae 93
Herre, Albert W. C. T. 392
Hesler, Lex R., work of 331
Heydrich, F., work of 93
Hill, T. G., work of 261
Hilleria 93
Hoffman, Conrad 244
Holden, Ruth 56, 335
Hooker, Sir Joseph Dalton, sketch of 384
Hori, S., work of 85
Horkelia **beneolens** 374
Houard, C., work of 468
Howell, Thomas, sketch of 458
Hutchinson, J., work of 93
Hybrids, Nicotiana 405
Hydrodictyon **africanum** 74
Hydrophyllaceae 92

I

Illinois Academy of Science 403
Indiana Academy of Science 330

Digitized by Google

Inheritance in maize 404
Insects and plants, homologizing of 462
Isle Royale, climax forest of 1, 115, 189

J

Jamaica, lichens of 332
Janet, Charles, "Le Volvox" 403; work of 462
Javillier, M., work of 88, 89, 90
Jeffrey, E. C. 168, 170, 175; work of 172
Johnson, A. G., work of 331
Jongmans, W. J., "Die palaeobotanische Literatur" 463

K

Klebs, G., work of 334
Kneucker, A., work of 93
Knight, Lee I. 337
Knot diseases of citrus trees 407
Koehne, E., work of 94
Koorders, S. H., work of 462
Kossowicz, A., work of 91
Krause, K., work of 94, 462
Kusano, S., work of 468

L

Lambert, F. D., work of 94
Land, W. J. G. 439
Lang, William H., work of 262
Lasiosphaeria 332
Lauterbach, C., work of 462
Layering in black spruce 452
Leaf fall, cause of 175
Lecanora melanophthalma 396; rubina 396; *thamnina* 395
Lecidea atrobrunnea 393; plana 394
Ledum 93
Lendner, A., work of 465
Lespedeza 92
Léveillé, H., work of 94
Lewis, I. W., work of 467
Lichens 92; antarctic 259; of Jamaica 332; of Mt. Rose, Nevada 392
Lignier, O., work of 263
Linnaeus, sketch of 330
Lipman, Chas. B. 409
Livingston, B. F., work of 263, 264
Loew, Oscar, work of 96, 174
Lupinus 93, 332

M

Macbride, J. Francis 372
Macfarlane, J. M., work of 94
Mackensen, B., work of 94
Macrozamia Moorei 141
Maiden, J. H., work of 94
Maize, inheritance in 404; origin of 261
Malt-diastase, effect of chlorides 265
Martin, John N. 96, 174
Massee, G., work of 94
Mathers, Frank, work of 331
Maytenus **enantiophyllus** 432
McCulloch, Lucia, work of 257
McLean, R. C., work of 262
Meliosma **Ronduzii** 432
Merrill, E. D., work of 94
Mesoxylon 171
Metabolism of fungi 85
Miller, F. A., work of 331
Mitlacher, Wilhelm, "Die offizinellen Pflanzen und Drogen" 403
Molisch, Hans, "Leuchtende Pflanzen" 253
Moreau, F., work of 465
Morphology of orchids 256
Morton, Friedrich, work of 470
Mosses 93; ecology of 96
Mucors 463
Murrill, W. A., work of 332
Musci 463
Myrica, root tubercles of 254

N

Namyslowski, B., work of 465
Nawaschin, S., work of 94
Nelson, Aven 372
Nematothecium 333
Némec, B., work of 94, 472
Nemophila **explicata** 377
Neopatersonia 332
Neutral salts, effect of 174
New Guinea, flora of 462
New Jersey, pine barrens of 260
Newman, L. H., "Plant breeding in Scandinavia" 328
Nichols, George E. 249
Nicotiana, hybrids 405; inheritance of flower size 177
Nitella 92
Nouhuysia 462
Nuclei of Protista 254

O

Ophioglossaceae, vascular anatomy of 262
Ophioglossum, a protocorm of 155
Opuntia 94
Oranges, cytology of seedless 260
Orchidaceae 92
Orchids, from Central America 332; morphology of 256
Oreocarya **cilio-hirsuta** 378
Oreodoxa 92

Digitized by Google

Orton, C. R., work of 331, 332
Osawa, I., work of 260
Osner, Geo. A., work of 331
Osterhout, W. J. V. 446
Ovarial injections 173
Owens, Charles E., work of 331
Oxyrhynchus 92

P

Paleobotany, literature on 463; notes on 335
Palm, a new Cretaceous 336
Parajaeschkea 332
Parasitic seed plants 252
Parish, S. B. 300
Parosela, Californian species 300; californica 309; californica **simplifolia** 309; Emoryi 306; Johnsonii 308; Johnsonii **minutifolia** 308; Johnsonii **pubescens** 308; Johnsonii **Saundersii** 308; mollis 302; **neglecta** 306; **Orcuttii** 305; Parryi 303; polyadenia 305; polyadenia **subnuda** 305; *Saundersii* 308; Schottii 309; Schottii **puberula** 312; spinosa 312; *Wheeleri* 308
Parrya Menziesii lanuginosa 374
Peklo, J., work of 254
Peltandra virginica 92
Penstemon perpulcher **pandus** 382; **rex** 381
Peperomia 93
Periodicity of tropical vegetation 333
Perkins, J., work of 462
Perymenium **ruacophilum** 437
Petry, E. J., work of 331
Petry, Loren C. 155
Phacelia **foliosepala** 377
Phloem of dicotyledons 236
Phomopsis citri 93
Phoradendron 94
Phosphorescence in plants 253
Photometric leaves and shoots 408
Phyllocarpus, seedling of 460; **septentrionalis** 433
Physcia tribacia 396
Picea mariana, layering in 452
Pilea 93
Pilger, R., work of 94
Pine-barrens of New Jersey 260
Plant associations of Delaware Coast 45
Plant breeding in Sweden 328
Plantago 94
Plants and insects, homologizing of 462
Plasmolysis, protoplasmic contractions resembling 446
Poria **atrosporia** 399
Porsch, O., work of 258
Potentilla *dichroa* 375; glomerata **dichroa** 375
Pott-Leendertz, R., work of 92
Preston, Howard W., "Key to the trees" 330, 402
Prothallia, fossil 262
Protista, nuclei of 254
Protocorm, of Ophioglossum 155
Puccinia 332
Pulle, A., work of 462

Q

Quehl, L., work of 332

R

Radlkofer, L., work of 94, 462
Ranunculaceae, embryogeny of 264
Ray tracheids in Coniferales 56
Rea, C., work of 332
Reed, Howard S. 421
Rehder, A., work of 94, 332
Revegetation of a denuded area 80
Reviews: Arber's "Natural history of coal" 170; Balls's "Cotton plant in Egypt" 329; Clements, Rosendahl, and Butters' "Minnesota trees and shrubs" 330; Collins and Preston's "Trees of the northeastern United States" 330, 402; Glück's "Wasser- und Sumpfgewächse" 328; Greene's "Carolus Linnaeus" 330; Haberlandt's "Physiologische Pflanzenanatomie 402; Hartman's "Protistenkerne" 254; Heinricher's "Parasitischen Samenpflanzen" 252; Janet's "Le Volvox" 403; Jongmans' "Die palaeobotanische Literatur" 463; Mitlacher's "Die offizinellen Pflanzen und Drogen" 403; Molisch's "Leuchtende Pflanzen" 253; Newman's "Plant breeding in Scandinavia" 328; Ridgway's "Color standards and color nomenclature" 461; Russell's "Soil conditions and plant growth" 167; Saccardo's "Sylloge Fungorum" 331
Rheedia **paniculata** 431
Rhododendron 332
Ricker, P. L. 461
Riddle, L. W., work of 332
Ridgway, Robert, "Color standards and color nomenclature" 461
Rigg, George B. 314
Ritter, G. E., work of 91
Robert, Mlle., work of 85, 86
Rombach, Sara, work of 258
Root-tubercles of non-leguminous plants 254
Rosaceae 94
Rosendahl, C. O., "Minnesota trees and shrubs" 330

Digitized by Google

Rosenstock, E., work of 462
Rubiaceae 463
Rudbeckia 332
Russell, Edward J., "Soil conditions and plant growth" 167

S

Sabulia 336
Saccardo, P. A. "Sylloge Fungorum" 331
Safety razor for hand-sections 399
Salts, toxic 409
Santon, B., work of 86, 87, 88
Sapium 93
Sargent, C. S., work of 94
Saxifragaceae 94
Schlechter, R., work of 332
Schneider, C., work of 94
Schönland, S., work of 332
Scott, D. H., work of 171, 472
Seaver, F. J., work of 332
Seedlings, influence of adult on 261; in liquid culture solutions 244
Seeds, dispersal by ants 470
Sernander, R., work of 470
Setchell, W. A., work of 94
Seward, A. C., work of 259
Sharp, Lester W. 256, 258
Sherff, E. E., work of 332
Shreve, Forrest, work of 263
Sieve tubes, evolution of 236
Sinnott, E. W. 472
Siphonella 93
Skan, S. A., work of 332
Slosson, M., work of 332
Smith, A. M., work of 334
Smith, Erwin F., work of 257
Smith, Huron H. 458
Smith, John Donnell 431
Smith, J. J., work of 462
Smith, W. W., work of 332
Smoke, toxicity of 337
Snow, Laetitia M. 45
Soil fertility 167
Solanum 92
Sorolpidium Betae 94
Souèges, R., work of 264
Speare, A. T., work of 332
Spratt, Ethel R., work of 255
Standley, P. C., work of 332
Stapp, Gail M., work of 331
Starr, Anna M. 251
Staurothele umbrina 393
Stemonitis nigrescens 400
Stephani, F., work of 333
Stephens, Edith L., work of 336
Stevens, Neil E., work of 256, 336
Stomata, comparative anatomy of 258
Stopes, Marie C., work of 335
Striga, haustorium of 336
Struthiopteris 92
Sturgis, W. C. 400
Successions on Isle Royale 115
Suringar, J. V., work of 462
Sutcliffia 175
Sweden, plant breeding in 328
Sydow, H. P., work of 333
Sylloge Fungorum 331
Symbolae Antillanae 254
Symplocaceae 92

T

Taylor, Norman, work of 260
Tenny, L. S., work of 407, 466
Theissen, F., work of 333
Thoday (Sykes), Mary G., work of 171
Thomas, H. Hamshaw, work of 264
Thompson, W. P., work of 172
Toxic inorganic salts and acids 409
Tower, W. L. 174
Tradescantia, effect of bog waters on root hairs of 314
Transeau, Edgar N. 66
Transpiration of apple leaves 421
Trees, key to 335, 402
Tropical vegetation, periodicity of 333

U

Urban, I., "Symbolae Antillanae" 254

V

Valeton, Th., work of 462
Van Hook, J. M., work of 331
Van Leeuwen, W. Docters, work of 262; Reijnvaan, W. Docters and J., work of 468
Vanoverberghia 94
Varga, Oskar, work of 175
Vermoesen, Camille, work of 256
Viola 92
Volkens, G., work of 333
Volvox 403

W

Warncke, Frederick, work of 258
Water plants, ecology of 327
Water relations of plants 264
Weingart, W., work of 333
Wernham, H. F., work of 333
Wherry, Edgar T., work of 335
Wiegand, K. M., work of 93, 333
Wiesner, J. v., work of 408
Williamsonia, a new 259
Wilson, E. H., work of 94
Wilson, Frank H. 409

Digitized by Google

Woburnia porosa 336
Wootonella 332
Wright, H., work of 334

X

Xanthoria lychnea laciniosa 396

Y

Yamanouchi, Shigéo 74

Z

Zeh, W., work of 333

Digitized by Google

Digitized by Google

Digitized by Google

Digitized by Google

Digitized by Google

Digitized by Google

Digitized by Google

Digitized by Google

Digitized by Google

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